Investigating the efficiency of reforestation approaches in restoring rainforest biodiversity and function

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September 2016

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Thesis submitted for the degree of Doctor of Philosophy

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September 2016

Declaration

I hereby declare that this work has been originally produced by myself for the present thesis and that it has not been submitted for the award of a higher degree to any other institution. Collaborations with other researchers, as well as publications or submissions for publications are properly acknowledged throughout.

Mia A. Derhé

Lancaster University, September 2016

ACKNOWLEDGEMENTS

I would like to thank my funders - the National Environment Research Council (U.K.), without which this project would not have been possible. I am also grateful to Lancaster University for providing me with additional funding for conference attendance.

I am very grateful to my supervisors Rosa Menéndez, Helen Murphy, Kate Orwin, Mike Lawes, Noel Preece and Andy Wilby. First of all I thank Rosa, for her patience and support throughout my PhD. Despite being a world away for the majority of my PhD I always felt fully supported as Rosa was always available for advice, assistance and encouragement. I am also very grateful to Rosa for the freedom which she granted me and the encouragement she offered to pursue my own research interests and expand my ideas. The speed with which Rosa returned my work with useful comments and advice always astounded me, particularly given the time different between us, and was a crucial element of my completing my thesis in time. I also thank Helen Murphy for always being on hand to offer support, assistance and practical advice on the ground in Australia. I am very grateful to Helen for her ever-helpful suggestions, detailed contributions to my manuscript, and general support – both emotional and practical. I also thank Helen and the rest of the staff at CSIRO, Atherton, for providing me with a welcoming workplace and a ‘home away from home’, where I always felt supported and accepted. Without the collaboration with CSIRO and their wonderful staff, this project would have been incredibly difficult and isolating. I am grateful to Noel Preece for his useful comments and advice on everything from survey design to my thesis structure. I also thank Noel for his support and guidance, particularly in the field, and for his many days spent helping me to carry mammal traps and on training me on mammal identification. I also thank Kate Orwin and Mike Lawes for their guidance and technical assistance on all leaf litter decomposition matters, as well as advice on chapter structure and helpful contributions to my manuscripts. I also thank Mike and Noel for their pivotal roles in obtaining the relevant ethics permission, permits and licences needed to conduct my work. I am indebted to Geoff Monteith for the hours he spent training me on dung beetle identification, as well as his invaluable help, advice and fascinating insight on anything invertebrate-related. I also thank Geoff for his tireless enthusiasm and for being such an inspiration in the field of entomology.

I gratefully thank all the landowners who allowed me unlimited access to their properties, without which this study would not have been possible. I would like to dedicate this work to the memory of Ian Freeman, who granted me unlimited access to his property for fieldwork, as well as providing me with a beautiful place to spend my time and marvel at the

resilience and beauty of nature. Ian was always ready to teach me about the history of the study area, talk about the logistics of forest restoration and his future plans for the creation of forest corridors. Ian had a contagious enthusiasm for forest restoration that inspired everyone he spoke to. I am forever grateful to Ian for sharing some of his light with me and for making my time on the Atherton Tablelands a brighter place. His legacy lives on in a beautiful piece of thriving rainforest that was once inhospitable, degraded pasture.

I thank Trees for Evelyn and Atherton Tablelands (TREAT), Tablelands Regional Council (TRC) nursery and QPWS Lake Eacham nursery, in particular Pete Snodgrass and Nick Stevens who were instrumental in helping me to establish a network of field sites for this project. I am very grateful to Dean Jones for his hours spent voluntarily training me on mammal handling and PIT tag insertion in the field, despite the injuries he sustained as a result. I am forever grateful to my wonderful friends Ryan Hart, Amy Vos, Avril Underwood, Sarah Hart and Jessica Tait for their voluntary fieldwork assistance, and for making days out in the field so much more fun.

I am forever indebted to the staff at the CSIRO Tropical Forest Research Centre, who welcomed me into their fold and accepted me as one of their own. My time at CSIRO has been instrumental in both my professional and personal development throughout my PhD. I am thankful to them for continuous support and advice over lunch and ‘smoko’ on presenting my work at conferences, teaching me about the dangers and pitfalls of fieldwork in the Wet Tropics, and for their countless stimulating discussions on everything from botany to the ecological role of feral pigs. I would also like to thank Dr Penny van Oosterzee for her support, guidance and assistance and her instrumental role in establishing the ARC project.

On a personal note I would very much like to thank all of the faraway friends that I have shared this journey with – particularly Amy Vos, Yoska and Karel Lindsay, Ryan Hart, Shane Savich, Gemma Horner and Avril Underwood who provided friendship, companionship, shoulders to cry on and so much fun when I was far from home. I also thank Ali Birkett for her invaluable help and assistance with everything PhD-related, and for always being there as a helpful colleague and a stoic friend. I would like to thank my family – both the old and the new, for their patience and understanding, for tolerating all of my tears and tantrums and for supporting me through the hardest times, particularly Mib, mum, dad, Rosie and the rest of the Rosamonds/ Millers. A big thank you goes to the smallest and most wonderful members of my family – Sienna, Didi, Poppy (and Juno) – for brightening the dark days with your smiles, cuddles and kisses.

Last but by no means least, I thank my (new) husband, Mark. I am forever grateful for your unfaltering love, support, patience, tolerance, understanding, and your willingness to move to the other side of the world for me. Thank you for pushing me when I wanted to give up. None of this would have been possible without your unwavering belief in me.

“It seems to me that the natural world is the greatest source of excitement;
the greatest source of visual beauty; the greatest source of intellectual interest.
It is the greatest source of so much in life that makes life worth living.”
— David Attenborough

ABSTRACT

Ecological restoration is being increasingly applied to reverse or mitigate biodiversity losses, re-instate ecological functions and increase the provision of ecosystem services in tropical forests. Effective assessment of the success of ecological restoration projects is critical in justifying the use of restoration, as well as improving best practice. However, there is often the assumption that once a degree of vegetation recovery occurs, diversity will increase, which equates with restoration of ecosystem functions. Since very few studies have investigated the interaction between the recovery of habitat structure, biodiversity and ecosystem functioning, this thesis aims to explore these mechanistic relationships to better understand the causal factors behind ecosystem recovery following restoration.

Both mammal and dung beetle community composition was clearly progressing towards that of rainforest with increasing restoration age. Restoration increased dung beetle-mediated secondary seed dispersal, leaf litter decomposition rates and decomposition multifunctionality (dung and litter decomposition).

Functional trait-based metrics provided a clearer pattern of mammal recovery than traditional species-based metrics. Functional diversity metrics were also better predictors of dung beetle-mediated functionality than species diversity metrics, emphasising the need to use a variety of ecologically meaningful diversity metrics when investigating the mechanisms and patterns driving ecological recovery.

In terms of vegetation structure, microhabitats were more complex and microclimatic conditions were more stable in restored sites and became more similar to rainforest with age. Faunal recovery was best explained by vegetation structure and microhabitat conditions; whereas functional recovery was explained by a combination of vegetation structure, microhabitat, soil properties and landscape context. These findings suggest that although landscape context and intrinsic site characteristics affect restoration success, they can potentially be mitigated by the establishment of a well-developed, rainforest-like habitat structure and microclimatic conditions within restoration sites.

By taking a holistic approach, this thesis demonstrates that ecological restoration of tropical forests leads to the development of a structurally more complex, rainforest-like vegetation structure, a shift to more stable microclimatic conditions and increased availability of microhabitat resources. These successional changes lead to the recovery of functionally diverse, rainforest-like faunal communities and efficient ecosystem functions within a relatively short time frame (10-17 years).

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Chapter 1

General introduction

1.1 HABITAT LOSS AND BIODIVERSITY DECLINE

Globally, forests cover nearly one third of the land area and contain over 80% of terrestrial biodiversity (UN 2011). Tropical forests are considered biodiversity hotspots due to their exceptionally high species richness and biotic complexity (Gaston 2000, Myers et al. 2000), and provide significant local, regional and global human benefits through the provision of economic goods and ecosystem services, including storing more than half the world's carbon (Pan et al. 2011). Despite this recognition, tropical forest loss continues to increase (Ahrends et al. 2010, DeFries et al. 2010, Kim et al. 2015), with over half the tropical moist forest cover worldwide having now been cleared (Asner et al. 2009). The simultaneous decline of both forest quantity and quality is expected to lead to massive extinctions of many forest habitat species (Wright and Muller-Landau 2006). Indeed, habitat destruction and degradation are considered to be the major drivers of declines in tropical biodiversity worldwide (Nepstad et al. 1999, Brooks et al. 2002, Defries et al. 2004, Nelson et al. 2006, Fischer and Lindenmayer 2007, Jetz et al. 2007, Laurance 2007, Pereira et al. 2010, Rands et al. 2010).

A further impact of habitat loss is the disruption of ecosystem functioning through the alteration of diversity and extinction order (Larsen et al. 2005). Species declines lead to the loss of ecological interactions in which those species are engaged (Janzen 1974, Tylianakis et al. 2008, Aizen et al. 2012). The loss of these interactions disrupts the functioning of forests and their ability to provide important ecosystem services, as well as processes that maintain ecosystem integrity and resilience (Chapin et al. 2000, Duffy 2009).

1.2 ECOSYSTEM RESILIENCE AND NATURAL REGENERATION

Resilient ecosystems are complex adaptive systems that are capable of self-reorganisation in the aftermath of disturbance – the capacity to return, over time, to a state similar to the pre-disturbance state (Holling 1973, Levin 1998, Chazdon 2014). However, there is a limit to the resilience of tropical forests. Disturbance disrupts the forest regeneration cycle, and can lead to the breaking of this cycle completely. When this happens, forests lose their intrinsic capacity to regenerate, succession is arrested, and in some cases, a new type of ecosystem develops – an alternative stable state

(Holling 1973, Scheffer et al. 2001, Beisner et al. 2003, du Toit et al. 2004, Folke et al. 2004) such as an introduced grass-dominated ecosystem.

Although many degraded ecosystems can recover from major disturbances without human assistance on timescales of decades to half centuries (Aide et al. 2000, Finegan and Delgado 2000, Jones and Schmitz 2009, Letcher and Chazdon 2009), rates of forest recovery on cleared land are highly variable (Holl 2007, Chazdon 2008b, Goosem et al. 2016) and natural regeneration may not occur at all. In severely degraded systems, alternative stable states can make efforts to restore pre-disturbance communities very difficult (Fukami and Lee 2006). In such cases, a single intervention, such as simply removing human disturbance, may not suffice to induce forest regrowth and so restoration efforts focussing on restoring the relation between biodiversity and ecosystem functioning may be needed (Aerts and Honnay 2011).

1.3 ECOLOGICAL RESTORATION OF TROPICAL FORESTS

Ecological restoration, both within and outside protected areas, is being increasingly applied worldwide and is becoming regarded as a major strategy for reversing or mitigating biodiversity losses and increasing the provision of ecosystem services in tropical forests (Young 2000, Holl 2011, Holl and Aide 2011), including carbon sequestration and climate change mitigation (Harris 2008, Edwards et al. 2010). Changes in land use, agricultural land abandonment, emerging markets for carbon and the inclusion of restoration goals in global policies are generating new opportunities for forest restoration in the tropics (Ehrlich and Pringle 2008, Nellemann and Corcoran 2009, Edwards et al. 2010).

Ecological restoration is the process of assisting the recovery of the physical structure, biodiversity and ecosystem functions of a degraded, damaged, or destroyed ecosystem (SER ISPWG 2004, Galatowitsch 2012). Ecological restoration is a broad concept and restoration efforts range from simply removing human disturbances to facilitate natural recovery (“passive restoration” DellaSala et al. 2003, Rey Benayas et al. 2009) to active intervention by creating, directing and accelerating successional processes (“active restoration” Brown and Lugo 1994, Goosem and Tucker 1995, Tucker and Murphy 1997, Goosem and Tucker 2013). An increasingly popular method of ecological restoration, particularly in the tropics, is reforestation (Chazdon 2008a), which is the re-establishment of tree cover to land previously cleared of rainforest. Ecological reforestation is an active, human-assisted restoration process by which multiple native tree species are planted in areas from which they have been previously cleared (Goosem and Tucker 1995, Erskine 2002, Kanowski et al. 2003, Lamb and Gilmour 2003, Catterall et al. 2004, Lamb et al. 2005, Goosem and Tucker 2013).

1.4 CURRENT UNDERSTANDING OF RESTORATION

The high species diversity and complexity of rainforests mean that recreating self-sustaining rainforest ecosystems in place of degraded habitat is a complex and difficult goal to achieve (Goosem and Tucker 1995, Kanowski et al. 2003). With such an array of reforestation styles and approaches available, conservation planners need an understanding of the factors affecting the success of rehabilitation, including the capacity of restored areas to develop on a trajectory towards native forest for both biodiversity and ecological functioning (Chazdon et al. 2009b, Gardner et al. 2009).

The success of restoration projects can be measured by many parameters, and a combination of vegetation structure, faunal composition and ecological function has been suggested as a minimum set of attributes with which to assess restoration progress (Reay and Norton 1999, Wardell-Johnson et al. 2001, Ruiz-Jaen and Aide 2005, Kanowski et al. 2007). During the past decade, the majority of studies assessing restoration success have focused largely on the recovery of vegetation structure and plant diversity, with relatively little attention paid to the recovery of faunal (particularly invertebrate) diversity or functional responses (Ruiz-Jaen and Aide 2005, Majer 2009, Brudvig 2011, Montoya et al. 2012).

In restoration ecology there is often the assumption that faunal diversity and ecological processes will return once a degree of vegetation recovery occurs (Majer 2009). However, studies on faunal responses to restoration show that faunal recovery is a complex process that is influenced by a number of biotic and abiotic factors, including habitat connectivity, proximity to rainforest and landscape context (Grimbacher and Catterall 2007, Nakamura et al. 2008, Golet et al. 2011, Munro et al. 2011).

1.5 BIODIVERSITY – ECOSYSTEM FUNCTION PERSPECTIVE

During the last two decades the positive relationship between biodiversity and ecosystem functioning (BEF) has been demonstrated through experiments manipulating species composition in model assemblages, primarily grasslands

(Loreau and Hector 2001, Hooper et al. 2005, Cardinale et al. 2012). Species composition, richness, diversity, evenness, and interactions all respond to and influence ecosystem properties and can enhance ecosystem functioning (Hooper et al. 2005, Cardinale et al. 2012). Although most research has concentrated on changes in richness and composition at the species level, these components of diversity are not always the most important (Hooper et al. 2005). Community ecologists are increasingly realising that a trait-based, causal view of community diversity may be more meaningful than species richness or composition (McGill et al. 2006).

The range of functions provided by a community is thought to depend primarily on the diversity of functional traits or values of key traits and the diversity of species that express them (Chapin et al. 2000, Díaz and Cabido 2001, Hooper et al. 2005, Prinzing et al. 2008, Cadotte et al. 2011, Cardinale et al. 2012) rather than the taxonomic identity of organisms. Functional traits operate in a variety of contexts, including competition, facilitation, mutualism, disease, and predation (Hooper et al. 2005), so in order to understand how changes in diversity and composition influence ecosystem properties, an understanding of the functional traits of the species involved is required. Functional trait-based metrics capture differences in species' morphology, life-history traits and ecological niches which affect community responses to disturbance (Gerisch et al. 2012) – complexities which traditional taxonomic indices do not capture. The current body of research looking at how biodiversity affects functioning of ecosystems has focused mainly on grassland systems (Tilman et al. 1997, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, de Bello et al. 2010, Cardinale 2011, Cardinale et al. 2012) and there is little information regarding the relationship between animal diversity and ecosystem functioning (Duffy 2003).

Restoration ecology has recently begun to adopt insights from the integrated BEF perspective (Naeem and Wright 2003, Naeem et al. 2009, Wright et al. 2009, DeClerck et al. 2010), and restoration projects are increasingly focussing on creating stable, resilient, functioning ecosystems (Thorpe and Stanley 2011). Although restoration of functional trait diversity over time implies increasing ecosystem complexity and functionality (Palmer et al. 1997, Aerts and Honnay 2011), this 'intrinsic' link is rarely tested, and the relationship between ecosystem functioning and functional diversity has received very little attention in a forest restoration context to date (Aerts and Honnay 2011). Furthermore, the BEF relationship is known to be complex and context dependent (Naeem and Wright 2003, Griffiths et al. 2014, Gagic et al. 2015), and understanding of the ecological processes underlying functional recovery remains incomplete and poorly integrated across different ecosystems (Ruiz-Jaen and Aide 2005, Montoya et al. 2012).

1.6 FUNCTIONAL DIVERSITY AND FUNCTIONAL TRAITS

The trait, or functional, structure of species assemblages is increasingly being used to understand community assembly processes (Mason et al. 2005, Kraft et al. 2008, Prinzing et al. 2008, Cornwell and Ackerly 2009) and how they may affect ecosystem function (Loreau et al. 2001, Belmaker and Jetz 2013). Functional diversity can be broadly defined as the value, range, and distribution of functional traits of organisms in a community (Tilman et al. 1997, Mouchet et al. 2010). Functional diversity is increasingly used in the analysis of biodiversity patterns and their links with various ecosystem functions (Tilman et al. 1997, Hooper and Vitousek 1998, Garnier et al. 2004, Díaz et al. 2007).

Gathering species into user defined functional 'groups' or 'guilds' results in the loss of information (Villéger et al. 2008) and the subjective imposition of a discrete structure on functional differences between species, which are usually continuous (Gitay and Noble 1997, Fonseca and Ganade 2001). Consequently, a suite of continuous multi-trait indices of functional diversity that directly use quantitative values for functional traits have been developed that have the potential to reveal community assembly processes (Mason et al. 2005, Mason et al. 2013). These indices can be used in conjunction to complementarily describe the distribution of species and their abundances within functional space (Mouchet et al. 2010).

In this thesis I shall be using four complementary functional diversity indices which describe the functional trait space occupied by a community (functional richness); the distribution of species' abundances throughout the occupied functional trait space (functional evenness); the variation in the distribution of species abundances with respect to the centre of functional trait space (functional divergence) (Villéger et al. 2008); and the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (functional dispersion) (Laliberté and Legendre 2010).

1.7 STUDY SITE – THE WET TROPICS

Listed as a World Heritage Area in 1988, the Wet Tropics region of tropical Australia (Figure 1.1) contains the oldest continually surviving tropical rainforest on earth and is one of the world's biodiversity hotspots. Although the Wet Tropics comprise less than 1% of the continents land area, they sustain the highest diversity and endemism of any terrestrial habitat (Keto and Scott 1986), with 107 mammal species (11 endemic), 368 bird species (11 endemic), 113 reptile species (24 endemic), 51 species of amphibians (22 endemic) (Williams 2006, Stork et al. 2011), over 2,800 plant species from 221 families (more than 700 species of which are endemic) (WTMA 2004).

The largest area of upland rainforest within the Wet Tropics occurs within the Atherton Tablelands (Bell et al. 1987, Williams et al. 1996) making it an important area to sustain viable populations of vertebrates (Williams et al. 2009). The Atherton Tablelands are also a key centre of endemism, with high levels of both vertebrate (Moritz et al. 2001) and invertebrate endemism (Yeates et al. 2002). The subregion also supports numerous mammal species with highly restricted geographical and elevational ranges (Winter 1988, Williams and Pearson 1997, Kanowski et al. 2001), as well as Australia's most diverse assemblage of sympatric marsupial folivores (Laurance 1989).

Vegetation clearance is the most significant threat to rainforests in the Wet Tropics, with more than half of the 640,000 ha of forest on freehold land being cleared over the last century, averaging 1,661 ha cleared per year over the last two decades (Department of Environment and Resource Management 2009).

Logging of the Atherton Tablelands began in the 1870s, progressing to broad-scale deforestation by the 1920s, mainly for dairy farms (Gilmore 2005), due to the favourable topography, high soil fertility and high annual rainfall of the area (Winter et al. 1987). This clearance has led to relic populations of many endemic plants and animals occurring in remnant forest patches, forming a fragmented mosaic structure consisting largely of pasture (Laurance 1991b, Crome and Bentrupperbaumer 1993, Laurance and Laurance 1996). Pasture areas were mainly used for cattle grazing, and by the end of the century were dominated by non-native tropical grasses, such as signal grass (*Urochloa decumbens*) and pasture legumes, with guinea grass (*Megathyrsus maximus*) and setaria (*Setaria sphacelata*var. *anceps*) also widely established, together with a large variety of other planted and invasive species.

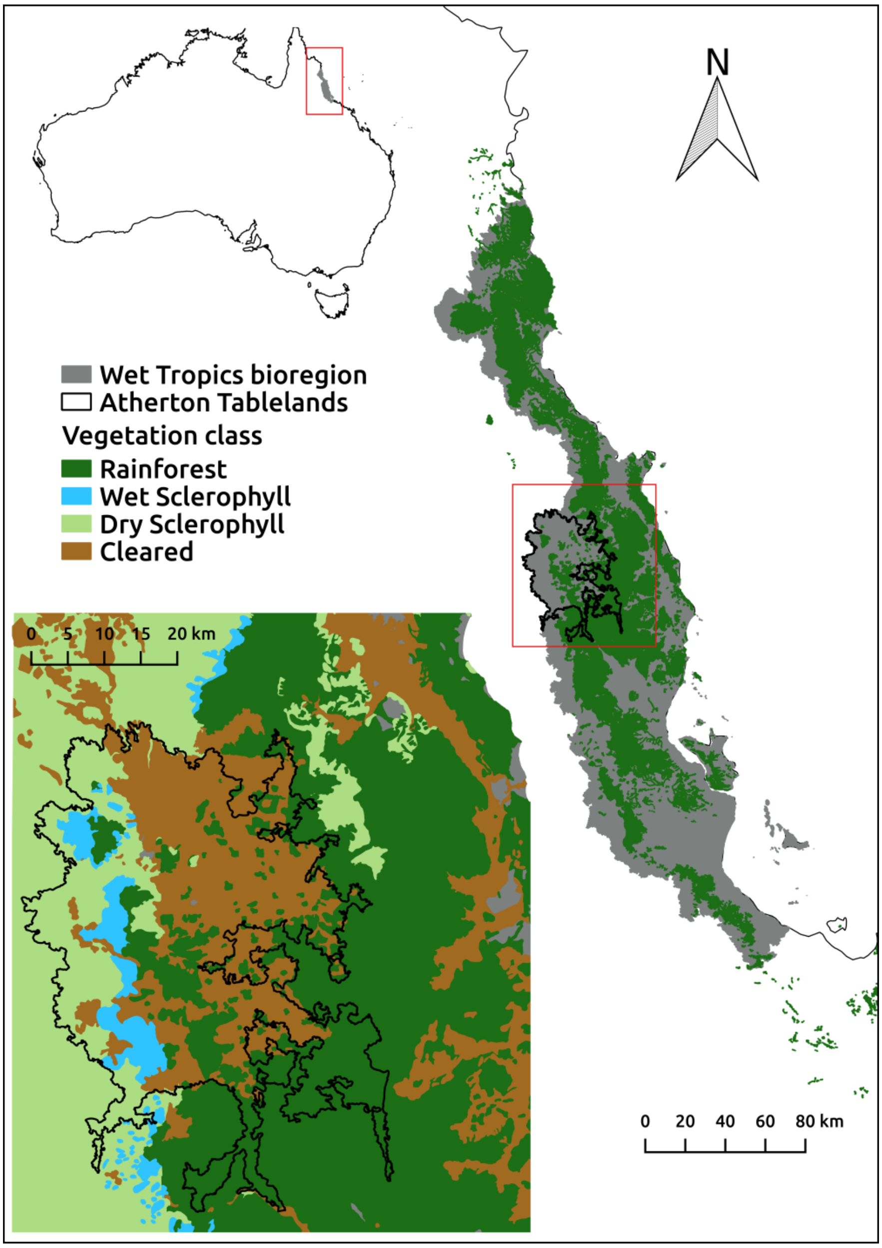

Figure 1.1 Map showing the location of the Wet Tropics region within Australia, and the location of the Atherton Tableland study area within the Wet Tropics. Areas of cleared forest, dry sclerophyll forest, wet sclerophyll forest and rainforest shown within the Atherton Tableland study area.

Clearing and cattle grazing on previously forested land in north Queensland results in altered tree species compositions, partially removed and heavily compacted top soils, altered nutrient cycles and deteriorated soil hydraulic properties (Congdon and Herbohn 1993, Holt et al. 1996). Pasture abandonment commenced in the 1940s, with larger transitions occurring from the 1980s onwards as declining productivity and economic realities forced dairy farmers out of the industry (Gilmore 2005).

Natural recruitment of native tropical rainforest species in abandoned pasturelands is a very slow process (Aide et al. 1995). Though reliable information on abandonment is not available, the regrowth rate in the Wet Tropics is known to be extremely slow, with some abandoned pastures not exhibiting any natural regrowth of (mesophyll type) forest trees even after 40 years (Florentine and Westbrooke 2004, Rasiah et al 2004). A realisation of the need to assist natural regeneration, along with an increased understanding of the effects of forest degradation and fragmentation on native biodiversity has led a variety of landholders, community groups and organisations throughout the region to replant forests for production, biodiversity and other conservation reasons (Goosem and Tucker 1995, Catterall et al. 2004). As a result of these reforestation activities, regrowth and replanted forests now make up around 100,000 ha of the 350,000 ha of rainforest and wet sclerophyll forest currently growing on freehold land in the region (Preece et al. 2012).

In general, two approaches have been followed in restoration programs. The first, direct seeding, is less expensive, but has the major disadvantages of poor germination, high mortality of seedlings, and severe weed competition (Evans, 1982). The second approach, transplanting seedlings raised in nurseries (Evans 1982), is more widely followed in restoration programs. Transplanting seedlings into abandoned or degraded lands helps to accelerate the recovery process and can also foster the establishment of species that exhibit different ecological characteristics features and that are capable of creating a favourable microclimate (by producing quick canopy closure). The seedling also can act as a ‘bait’ crop in attracting a frugivorous fauna, which can enhance the natural dispersal of seed on the site (Goosem and Tucker, 1995). Goosem and Tucker (1995, 2013) proposed two major types of tropical rainforest restoration for use in Australian systems: (1) the framework species method; and (2) the maximum species diversity method (Goosem and Tucker 1995). In the framework species method, one or a group of fast growing species is planted to provide a dense canopy that will suppress weed species in a short period of time (approximately 1.5 to 2 years). The major advantages of this technique are that it needs only a single planting and it is self-sustaining. However, this technique is only suitable to areas where native vegetation, with a good source of propagules, is located close by. In the maximum species diversity method, a larger percentage of species is from the mature phase and primary promoters are generally avoided. The major disadvantage is a slower growth rate, which requires intensive post-planting management. However, this method quickly creates species-rich forest communities, with less dependence on subsequent colonisation from nearby natural forests (Goosem and Tucker 1995, 2013). This study uses restoration sites that have been planted using transplanted seedlings and the maximum diversity method to assess the effectiveness of reforestation approaches in restoring rainforest biodiversity and function.

1.7.1 Study design

A network of sites was established on the Atherton Tablelands composed of a reforestation chronosequence (12 restoration planting sites, 2 - 17 years since planting), along with two reference conditions (ungrazed, abandoned pasture and intact, remnant rainforest).

Restoration sites were categorised into young (1-5 years), mid-age (6-12 years) and old (13-17 years) restoration categories. Reforested sites were on once-forested land which had endured an intervening period of clearing, followed by typically 30–60 years of intensive cattle grazing. Prior to restoration planting, grasses, herbs and other low-growing pasture-associated plants were suppressed with repeated herbicide applications of either glyphosate (which has a broad spectrum action on all types of plant) or the grass-selective Fusilade (fluazifop-p butyl) and Verdict (haloxyfop-R-methyl). Native tree seedlings were cultivated in nurseries using seeds from local type specimens harvested in nearby intact forest. Seedlings were transplanted after they had been established in 140 mm diameter pots and reached 200 – 700 mm in height. Transplanted seedlings were hand planted into machine-augered holes, watered immediately after planting and surrounded by mulch. Typically, plantings were established by regional agencies or landholders and were of 20–50 species of saplings (mean 30 species) of locally native tree species spaced 1.75 m apart (Freebody 2007; Goosem & Tucker 2013). Maintenance was conducted for 2–4 years after planting to enable tree survival. In this study, restoration sites were selected to ensure they were planted at the same densities and diversities (as much as possible) and contained a relatively high proportion of the same species. In order to do this, sites were located within similar vegetation types. The most commonly planted species in the restoration sites were *Guioa lasioneura* (Sapindaceae), *Alphitonia petriei* (Rhamnaceae), *Casuarina cunninghamiana* (Casuarina), *Elaeocarpus angustifolius* (Elaeocarpaceae), *Homalanthus novoguineensis* (Euphorbiaceae), *Terminalia sericocarpa* (Combretaceae), *Cardwellia sublimis* (Proteaceae), *Neolitsia dealbata* (Lauraceae), *Flindersia brayleyana* (Rutaceae), *Acronychia acidula* (Rutaceae), *Ficus spp* (Moraceae), *Acacia spp*. (Mimosaceae) and *Syzygium spp*. (Myrtaceae).

Each restoration site was 1.08 - 2.11 ha in size (mean 1.37 ha) and were of similar shape. Restoration sites were 0.2 - 2 km from any rainforest patch >200 ha (mean 0.5 km) and were and were all connected to a similar degree to large mature rain forest tracts by established restoration or remnant forest corridors. Restored sites were at least 500 m from another site of similar age (with different ages spatially interspersed as far as possible). Restoration sites were selected through discussions with landholders, community groups and regional agencies, and checked by examining vegetation maps and historical aerial photography.

To monitor the ‘success’ of a restoration planting, it is necessary to select a set of reference sites against which progress can be judged. Ideally, these reference sites should include sites that are representative of the pre-planting state (e.g. pasture) or control state (e.g. unassisted regeneration) as well as a number of sites representative of the target state (e.g. intact forest). Having reference sites at both ends of the spectrum enables assessment of how far the restoration planting has come from the pre-planting state, and how far it has to go to resemble an ‘intact’ forest system (Wardell-Johnson et al. 2001).

Remnant intact rainforest patches were considered as the reference target sites, representing the desired end point of restoration (n=4). Rainforests in the region are mostly complex notophyll to mesophyll vine-forest, characterised by a canopy range of 12 to 45 metres in height (Goosem and Tucker 2013). Rainforest reference sites had a closed canopy >20 m high and a high diversity of structural features, life-forms, and tree species. All rainforest reference sites were at least 300 ha in size.

All degraded pasture and restoration sites used in this study were previously tropical forest, which can have a slower recovery rate than other habitat types (often greater than 40 years) (Florentine and Westbrooke 2004, Jones and Schmitz 2009). Past land-use history is one of the most important factors determining recovery processes (Jones and Schmitz, 2009) and in this case, the pasture and restoration sites were cleared 80-150 years ago (Gilmore 2005), and were then grazed for extended periods (>70 years). Extended cattle grazing over a long time period is known to deplete the seed bank more than other land uses (e.g. selective logging or shifting agriculture) (Meli 2003, Holl 2007) and cause severe soil degradation and changes in soil hydrology (Congdon and Herbohn 1993, Holt et al. 1996), which severely hinders natural regeneration. Furthermore, when grazing animals are removed from pastures, aggressive exotic grasses can invade and arrest succession (reviewed in Holl and Cairns 2002), as is the case in the study area. In addition, the majority of pasture in the study area is several kilometres from the nearest sources of forest seeds, which greatly limits propagule availability and the potential for passive restoration (White et al. 2004). As such, abandoned, ungrazed pasture sites in the study area represented both a pre-planting reference state (pasture), as well as a control state (unassisted regeneration) (n=4). All degraded pasture sites had been ungrazed and abandoned for 3 - 10 years, were of similar size, ranged from 1.36 – 3.83 ha (mean 2.19 ha) and were 200 – 500 m from any rainforest patch >200 ha (mean 187 m). All pasture sites were connected to large mature rain forest tracts by established restoration or remnant forest corridors. Pasture reference sites all lacked trees and had dense grass dominated by non-native species (principally *Urochloa decumbens* but also *Megathyrsus maximus* and *Setaria sphacelata*).

Sample sites were selected to limit variability in soil type and elevation (all 704–1022 m) and minimise spatial interspersion among site types. Sites were set up in four blocks within the landscape (Figure S2.7 in Supporting Information), with each block containing one site of each of the three restoration categories and starting and reference sites. Blocks were selected to represent the maximum variation in topographic, climatic and geological parameters in the landscape so all sites within a block were similar in these parameters. All blocks were separated by >1.5 km

All sites were either on basalt soils (Blocks 1-3) or mixed basalt and granite (Block 4). The vegetation of the sites was comprised of three main types: complex mesophyll to notophyll vine forests usually on basalt tablelands (Blocks 1 and 3); Araucarian notophyll/microphyll and microphyll vine forests (Block 2); and wet tall open-forest, containing a well-developed understorey of rainforest components, including ferns and palms (Block 4) (Tracey and Webb 1975). Blocks differed significantly from one another in terms of elevation (704 – 2011 m) and slope (0.8 – 20.3°) (Table 1.1).

Table 1.1 Range of values of landscape metrics within each sampling 'block'. Generalised linear models (with appropriate error structures), followed up with a contrast analysis (using 'block' as a predictor, obtaining confidence intervals using parametric bootstrapping) were conducted to determine differences in values among 'blocks'. Means (± 1 SE) are shown and superscripts represent pairwise differences at the $P \leq 0.05$ level.

	Block 1	Block 2	Block 3	Block 4	Chisq	Df	*P*
% rainforest within 250m	25.40 ± 21.22	29.27 ± 13.71	28.80 ± 20.92	28.60 ± 20.51	0.02	3	0.999
Distance to rainforest (m)	616.01 ± 317.13	453.42 ± 433.44	230.38 ± 151.87	53.12 ± 22.61	3.48	3	0.323
Distance to pasture (m)	187.13 ± 185.45	60.21 ± 39.80	137.17 ± 104.16	134.04 ± 66.20	4.59	3	0.205
Area (ha)	82.22 ± 89.78	101.08 ± 111.50	97.12 ± 107.09	101.36 ± 111.42	0.03	3	0.999
Elevation (m)	720.64 ± 9.32^{a}	844.63 ± 40.99^{b}	791.68 ± 59.19^{ab}	1001.14 ± 9.25^{c}	37.61	3	<0.001
Slope	3.03 ± 1.36^{a}	8.84 ± 3.70^{ab}	3.77 ± 1.21^{a}	9.57 ± 0.70^{b}	10.90	3	0.012

1.8 STUDY TAXA AND ECOSYSTEM FUNCTIONS

The main goal of ecological restoration is the recovery of vegetation structure, species diversity and abundance, and ecological processes (Ruiz-Jaen and Aide 2005). This thesis therefore simultaneously assesses the recovery of each of these elements by looking at the response of several components of biodiversity from different levels within a trophic system, ecosystem functioning and habitat structure to tropical forest restoration.

1.8.1 Mammals

Mammals are particularly vulnerable to land use change (Tabeni and Ojeda 2003, Hoffmann et al. 2011) and are one of the biodiversity groups showing the most rapid global decline (Di Marco et al. 2012). Since forest mammal species are relatively specialised and intolerant of the surrounding landscape matrix, this makes them more prone to extinction (Laurance 1991a, Turner 1996). Small mammals, being comparatively easy to study, are therefore a good model to understand community patterns produced by the forest recovery process (e.g. Carey and Johnson 1995, Pinotti et al. 2015). Mammals are also key ecosystem function mediators, disseminating seeds and spores (Williams et al. 2000, Westcott et al. 2005, Westcott et al. 2009); enhancing nutrient cycling through the deposit of nutrient-rich dung (Bardgett et al. 1998), physically mixing soil, decomposed organic matter and litter (Fleming et al. 2014); providing prey for terrestrial and avian predators; regulating some invertebrate populations (Churchfield et al. 1991); and providing an important food source (in the form of dung) to dung beetles. Changes in mammalian community structure following ecological reforestation are therefore likely to have consequences for the integrity and stability of the system (Goheen et al. 2004).

Australia's highly distinctive and mostly endemic land mammal fauna has suffered declines, extirpations, range contractions and extinction. For some species the loss has been absolute, with 255 mammal species having gone extinct in the last 10,000 years (Turvey 2009), putting current Australian mammal extinction rates far higher than the average background extinction rate (Hoffmann et al. 2011). The extent of decline and extinction of mammals is greater than has been documented for any other taxonomic group in Australia (Woinarski et al. 2015). The drivers of these declines are varied and often cumulative, but habitat alteration and loss are the most widespread drivers (Rands et al. 2010, Lawes et al. 2015).

Australia's terrestrial mammal fauna is the most distinctive in the world, with 87% of species being endemic (Holt et al. 2013). The Atherton Tableland in the Wet Tropics region of far north Queensland has the highest diversity of non-flying mammals in Australia, including a number of restricted endemic species (Winter 1988, Kanowski et al. 2001, Williams 2006). This area also supports the largest area of upland rainforest within the Wet Tropics (Bell et al. 1987, Williams et al. 1996) making it an important area to sustain viable populations of vertebrates (Williams et al. 2009). Many rainforest mammals on the Atherton Tablelands are suffering declines, especially where populations are restricted within habitat fragments (Laurance 1991a, Laurance 1994, 1997). Furthermore, climate change is likely to exacerbate current mammal declines, with catastrophic losses due to climate change predicted to occur in the mammal fauna of high-altitude tropical rainforests of the Wet Tropics of Australia (Williams et al. 2003).

For this study, mammals were chosen as the vertebrate study taxa as they play an integral role within rainforest ecosystems, are particularly vulnerable to declines, range contractions and extinctions in Australia, and directly affect the dung beetle community through the dung that they provide. Therefore the inclusion of both mammals and dung beetles in this study provides an overview of the response of multiple trophic levels within the dung decomposition system.

1.8.2 Dung beetles

Dung beetles (Coleoptera; Scarabaeidae) are a large, functionally diverse and widely distributed group of insects that feed mainly on decomposing matter, mostly mammalian dung, carrion, decaying fruits and fungi (Hanski and Cambefort 1991). Dung beetles use mammalian dung resources for feeding and nesting purposes. Globally there are considered to be three functional guilds of dung beetles, based on their nesting strategy. Firstly, endocoprids, or 'dwellers' which lay their eggs within a dung deposit; paracoprids, or 'tunnelers', which bury brood balls directly beneath or beside the dung pile; and telocoprids, or 'rollers', which roll create brood balls and transport them some distance away from the dung pile before burying it (Halffter and Edmonds 1982, Hanski and Cambefort 1991, Holter et al. 2002). Australia dung beetle communities are comprised mainly of tunnelers and rollers species (Hanski and Cambefort 1991).

Dung beetles are sensitive to alterations in environmental conditions (Feer and Hingrat 2005, Scheffler 2005, Nichols and Gardner 2011) and rapidly respond to the effects of land use change including the destruction, fragmentation and isolation of tropical forest (Favila and Halffter 1997, Spector 2006, Braga et al. 2013, Edwards et al. 2014). These responses include reductions in abundances, as well as in taxonomic and functional diversity ((Halffter and Arellano 2002, Larsen et al. 2005, Gardner et al. 2008, Larsen et al. 2008, Barragán et al. 2011, Braga et al. 2013, Edwards et al. 2014). Dung beetle communities show distinct structure and species composition in disturbed habitats compared to those found in original forests (Howden and Nealis 1975, Davis et al. 2001, Nichols et al. 2007, Gardner et al. 2008, Hernandez et al. 2014) and so are particularly reliable indicators of tropical forest disturbance and land use change (Favila and Halffter 1997, Spector 2006, Gardner et al. 2008, Barlow et al. 2010, Nichols and Gardner 2011, Bicknell et al. 2014).

The evolutionary relationship between mammals and dung beetles dates to the Cenozoic (Cambefort 1991, Halffter 1991) and has long had an effect on structuring dung beetle communities. Consequently, dung beetles are also often considered a proxy for the wildlife communities (primarily large mammals) that provide the faeces upon which they feed (Hanski and Cambefort 1991, Nichols et al. 2009), making their value as indicators disproportionally high (Nichols and Gardner 2011). This dependency on mammalian dung (Halffter and Edmonds 1982) also makes dung beetles vulnerable to cascade effects, as evidence suggests that a decline in mammals disrupts the diversity and abundance of dung beetle communities (Estrada et al. 1999, Scheffler 2005, Andresen and Laurance 2007, Nichols et al. 2009, Barlow et al. 2010).

Dung beetles are an ideal focal taxa for elucidating the impact of restoration on biodiversity and ecosystem functioning as they are functionally diverse and taxonomically well characterised (Mcgeoch et al. 2002, Spector 2006, Nichols et al. 2007, Gardner et al. 2008), are sensitive to disturbance, relatively easy and inexpensive to sample, broadly distributed, community turnover occurs rapidly (Nichols and Gardner 2011) and they provide key ecosystem services important to forest dynamics (reviewed in Nichols et al. 2008).

1.8.3 Dung beetle meditated ecosystem processes

Dung beetles function as decomposers in tropical and temperate ecosystems, using decaying organic material as food for both larvae and adults. As such, dung beetles are important components of terrestrial ecosystems, providing a set of ecological functions important to forest dynamics, through their movement and consumption of mammalian dung. Dung removal and burial by dung beetles has many beneficial ecological consequences, such as soil fertilisation and aeration (Bang et al. 2005), improved nutrient cycling and uptake by plants (Yamada et al. 2007), secondary seed dispersal (Andresen and Feer 2005), biological control of pests and parasites (e.g. Bergstrom 1983), and providing prey for a range of birds and mammals (Nichols et al. 2008). As dung beetles break apart dung piles and distribute the material away from the source, they relocate seeds from the point at which they were deposited through defecation by other animals (secondary seed dispersal), which increases seed survival (Andresen and Levey 2004, Andresen and Feer 2005, Nichols et al. 2008).

Dung decomposition by dung beetles increases key soil nutrients, including nitrogen and phosphorus in soil (Bertone 2004, Yamada et al. 2007) and promotes aerobic respiration by increasing dung fragmentation and aeration (Stevenson and Dindal 1987, Rosenlew and Roslin 2008, Penttilä et al. 2013). The action of tunnelling and dung burial by dung beetles also instigates micro-organismal and chemical changes in the upper soil layers, aerates soils, improves water penetration and prevents nutrient loss (Brown et al. 2010).

The sensitivity of dung beetles to environmental change and their contribution to such a variety of important ecosystem processes means that dung beetle assemblages and dung beetle mediated ecosystem functions can both indicate and influence the success of restoration efforts.

1.8.4 Decomposition and nutrient cycling

Soil processes are essential in enabling forest regeneration in disturbed landscapes. Tropical rain forests generally exist on highly leached, nutrient-poor soils with relatively low soil organic matter (SOM) sinks. Litter fall and leaf decomposition represent one of the major pathways of nutrient cycling in tropical forests (Vitousek 1984, Aber and Melillo 1991, Gill and Jackson 2000), as nutrients and carbon released from decaying leaves create available nutrient pools for plants, and allow SOM formation (Eijsackers & Zehnder 1990). Nutrient cycling and decomposition underpin a number of ecosystem functions and services in tropical forests (MEA 2005) and the process of litter decomposition is paramount for restoring soil condition and continued plant and forest productivity (Swift et al. 1979, Defries et al. 2004, Moore et al. 2006, Li and Ye 2014). Nutrient cycling through decomposition determines how much organic and inorganic components are available for organisms to persist in an ecosystem (Davidson et al. 2004, Feldpausch et al. 2004) and are therefore important ecological processes that provide information on the resilience of restored ecosystems. As well as being key ecosystem functions, decomposition and nutrient cycling are vulnerable to anthropogenic activities. Decomposition rates decline with degradation and disturbance in rainforests and woodlands that have been subjected to logging (Parsons and Congdon 2008), burning (Silveira et al. 2009) and grazing (Lindsay and Cunningham 2009), as well as in monoculture plantations (Barlow et al. 2007).

1.9 RESEARCH OBJECTIVES AND THESIS STRUCTURE

Effective assessment of the success of ecological restoration projects is critical in justifying the use of restoration in natural resource management as well as improving best practice. Ecological restoration projects are increasingly focussing on creating stable, resilient, functioning ecosystems, however there are very few studies that investigate the response of both functioning and biodiversity of restored sites. In addition, there is often the assumption that increasing species and or functional diversity equates with restoration of ecosystem function, but there has been little research empirically demonstrating these mechanistic relationships *in situ*.

The overall objective of this thesis is to assess how several components of diversity from different levels within a trophic system respond to restoration, whilst simultaneously looking at the responses of ecosystem functions that relate to nutrient cycling and forest succession (Figure 1.2), and investigating the relationship between biodiversity and ecosystem functioning within a restoration context. In achieving this objective, the thesis addresses four principal research topics:

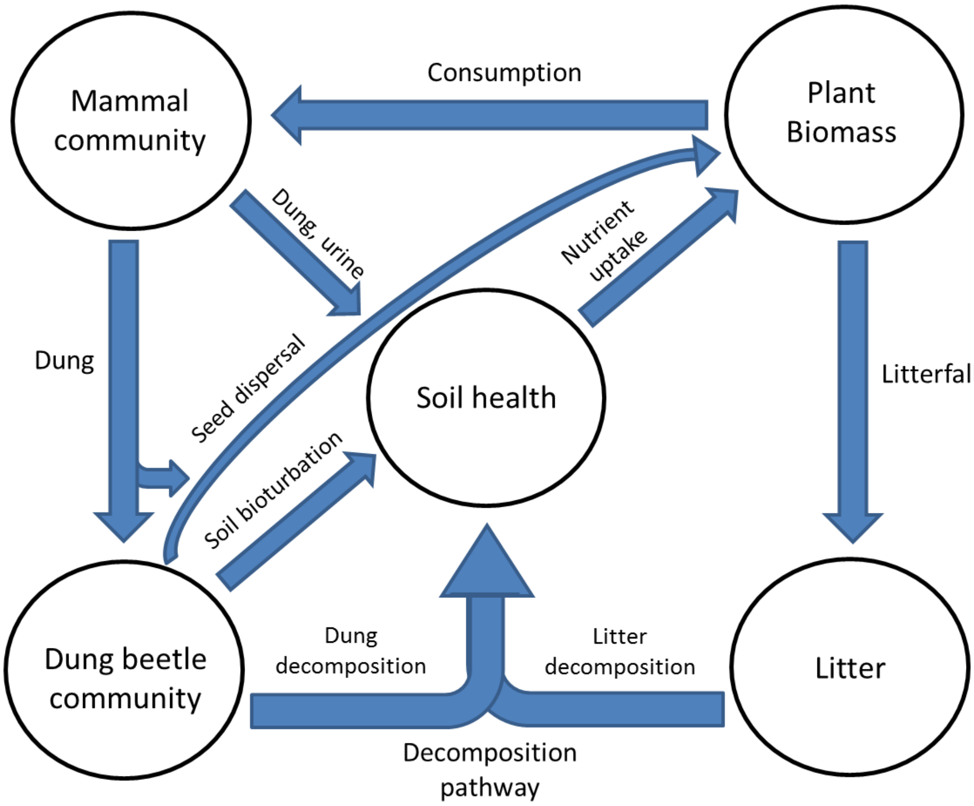

Figure 1.2 Simplified outline of the contribution of mammals, dung beetles and decomposition processes to the nutrient cycle affecting plant biomass in tropical forest systems

1.9.1 Chapter 2: Assessing responses of mammal diversity to tropical forest restoration: a functional approach

Faunal recolonisation following ecological reforestation is a major component of ecosystem recovery due to the ecological functions that they mediate. Mammals play an integral role within rainforest ecosystems as consumers, seed and spore dispersers and as predators and prey. Changes in mammalian community structure following ecological reforestation are therefore likely to have consequences for the integrity and stability of the system. This chapter examines: (1) whether small mammal species diversity increases with time since restoration; (2) whether functional diversity increases with restored forest age; and (3) whether restoration forests are converging in species composition and functional diversity on the 'old-growth' forest condition?

1.9.2 Chapter 3: Measuring the success of reforestation for restoring dung beetle diversity and associated ecosystem functioning

Functional trait information and diversity indices complement traditional taxonomic based indices and when used together with assessments of ecological functions, can provide comprehensive evaluations of the success of restoration projects. By directly measuring the response of dung beetle mediated ecosystem functions and dung beetle diversity to ecological restoration of tropical forests, the mechanistic link between biodiversity recovery and functional recovery is examined, using individual functions and an index of multifunctionality. This chapter examines: (1) whether increasing time since restoration leads to an increase in species diversity and a more rainforest-like community structure; (2) increasing time since restoration leads to an increase in functional diversity and functional efficiency; and (3) the relationship between biodiversity and ecosystem functioning in ecologically restored sites.

1.9.3 Chapter 4: Investigating Responses of leaf litter decomposition rates to tropical forest restoration and microhabitat conditions

Conversion of forest to agriculture is widespread and is known to cause substantial deterioration in soil properties. Therefore, the restoration or reforestation of tropical forest on degraded land requires the restoration of ecosystem processes that recover suitable soil conditions. Leaf litter decomposition is one of the major pathways of nutrient cycling, crucial for restoring soil condition, and as such provides an indication of nutrient cycling and soil quality, as well as the soil and decomposer subsystem. This chapter examines: (1) whether leaf litter decomposition rates increase with time since restoration started; (2) how the successional stage of restoration affects key biophysical parameters associated with leaf litter decomposition (mean temperature and humidity, variability in temperature and humidity, mean woody and leaf litter volume, soil pH and soil bulk density); and (3) the relationships between biophysical parameters and decomposition rate.

1.9.4 Chapter 5: Determining the biophysical drivers of biodiversity and ecosystem functioning recovery through ecological restoration

There are many factors that affect the successional trajectories of restored forests. All of these factors interact and influence the habitat characteristics of restored forests and, in turn, the recovery of biodiversity and functionality. This chapter looks at the responses of key biophysical characteristics to ecological restoration and explores the relationship between these characteristics and the recovery of biodiversity and functionality. Of particular interest is the relative importance of landscape and site variables (e.g. distance to mature forest, soil properties) that are independent of restoration, compared with habitat structure and microclimatic conditions (e.g. canopy cover, understory density, litter volume) that are affected by restoration, on biodiversity and functional recovery. This chapter examines: (1) how biophysical parameters (habitat structure, microhabitat conditions, soil properties and landscape context) respond to ecological restoration; (2) the effect of biophysical parameters on biodiversity and ecosystem functioning; and (3) whether restoration-dependent characteristics (i.e. habitat structure, microhabitat conditions) are more important than restoration-independent characteristics (i.e. soil properties, landscape context) in driving patterns of biodiversity and functionality recovery.

Each of the data chapters of this thesis have been written for publication: Chapter 2 is in preparation for submission to Restoration Ecology. Chapter 3 has been published in the Journal of Applied Ecology. I intend to submit Chapter 4 to Forest Ecology and Management, and Chapter 5 to Ecological Applications in due course. Therefore, this thesis is made up of stand-alone chapters linked by a common theme of the responses of biodiversity and ecosystem functions to tropical forest restoration. Chapter 6 summarises the key findings resulting from each chapter and highlights future research needs.

Chapter 2

Assessing responses of mammal diversity to tropical forest restoration: a functional approach

2.1 SUMMARY

- Ecological restoration is increasingly applied in tropical forests worldwide to mitigate biodiversity losses and recover ecosystem functions. In restoration ecology functional richness, rather than species richness, determines community assembly and measures of functional diversity provide a mechanistic link between diversity and the ecological functioning of restored habitat. Vertebrate animals are important for ecosystem functioning. Here, the functional diversity of small-to-medium sized mammals is examined, to evaluate both the diversity and functional recovery of tropical forest.
- The variation in mammal species diversity, species composition, functional diversity and functional composition along a restoration chronosequence from degraded pasture to ‘old-growth’ rainforest is assessed in the Wet Tropics of north-eastern Australia.
- Species richness, diversity, evenness and abundance did not vary, but total mammal biomass and mean body mass increased with restoration age. Species composition in the restored areas converged on the composition of rainforest sites and diverged from pasture sites with increasing forest restoration age.
- Functional metrics provided a clearer pattern of recovery than traditional species-based metrics, with most functional metrics significantly increasing with restoration age when taxonomically based metrics did not. Functional evenness and dispersion increased significantly with restoration age, and functional divergence was significantly higher in rainforest sites than pasture. The change in community composition represented a functional shift from invasive, herbivorous, terrestrial habitat generalists and open environment specialists in pasture and young restoration sites, to predominantly endemic, folivorous, arboreal and fossorial forest species in older restoration sites.
- *Synthesis and Applications*. Restored forests have the capacity to recover functionally diverse, rainforest-like mammal communities in a relatively short period of time (10-17 years), which aids the recovery of ecosystem functioning and thus ecosystem stability in recovering forests. These findings demonstrate that traditional species-based metrics of diversity are insufficient, and should be complemented with measures of composition, functional diversity and functional composition, to evaluate the efficacy of restoration practices.

Keywords: ecosystem functioning; ecological restoration; functional diversity; functional guilds; mammals; reforestation; trait-based metrics; tropical forest; wet tropics

2.2 INTRODUCTION

Half of the world's mammal species are declining and one-quarter face the risk of extinction (Schipper et al. 2008). Australia's highly distinctive and mostly endemic land mammal fauna has suffered greater declines, range contractions, and extinctions than any other taxonomic group, with more than 10% of the original 273 endemic mammals having suffered extinctions, the highest in the world in recent times (Lawes et al. 2015, Woinarski et al. 2015). The drivers of these declines are varied and often cumulative, but habitat alteration and loss are the most widespread drivers (Rands et al. 2010, Lawes et al. 2015).

As a means of reversing or mitigating such biodiversity losses, as well as recovering ecosystem processes and services, ecological restoration is being increasingly applied in tropical forests worldwide (Holl and Aide 2011). A popular method of ecological restoration, particularly in the tropics, is ecological reforestation (Chazdon 2008a), which is the re-establishment of native tree cover to land previously cleared of rainforest (Goosem and Tucker 2013). Faunal recolonisation following ecological reforestation is a major component of ecosystem recovery due to the ecological functions that they mediate. However, knowledge of faunal outcomes in ecological restoration plantings, and the factors that influence the direction of the restoration pathway, remains in its infancy (Catterall et al. 2012).

Mammals play an integral role within rainforest ecosystems as consumers, seed and spore dispersers and as predators and prey. Changes in mammalian community structure following ecological reforestation are therefore likely to have consequences for the integrity and stability of the system (Goheen et al. 2004). However, most studies on ecological restoration have focussed on the recovery of vegetation structure and floral species diversity (Brudvig 2011). Invertebrate and vertebrate animals are important for ecosystem functioning, so full evaluation of restoration success requires a more unified approach that integrates both floral and faunal approaches (McAlpine et al. 2016).

Although there have been studies of faunal recovery in restored sites in the Wet Tropics of Australia (e.g. (Nakamura et al. 2003, Catterall et al. 2012, Leach et al. 2013, Derhé et al. 2016), only two have examined the recolonisation of ecologically restored forests by mammals (Paetkau et al. 2009, Whitehead et al. 2014). The importance of replantings for gene flow in mammals has been highlighted in the resumption of movement through a restored corridor in the Wet Tropics between populations of two Rattus sp. that were previously demographically isolated from each other (Paetkau et al. 2009); and the recovery of small mammal community composition in restored sites has been demonstrated by Whitehead et al. (2014).

Two of the main goals of ecological restoration projects are the recovery of biodiversity and the creation of functioning ecosystems (Montoya et al. 2012). Effective monitoring should incorporate measures of both biodiversity and ecosystem functioning. The traits and niches filled by species determine how diversity influences ecosystem function, and community ecologists are increasingly realising that a trait-based or functional role approach to measuring community diversity may be more meaningful than traditional species richness or composition (McGill et al. 2006). Functional diversity, defined as the diversity and abundance distribution of traits within a community (Mason et al. 2005), provides a mechanistic link between diversity and ecological processes and is a more accurate predictor of ecosystem functioning than traditional species-based metrics (Cadotte et al. 2011, Mouillot et al. 2011, Mouillot et al. 2013, Derhé et al. 2016). Furthermore, functional diversity, rather than species richness, determines community assembly as it drives the processes that structure biological communities (Cumming and Child 2009, Mouchet et al. 2010).

This research builds on work by Whitehead et al. (2014) by evaluating the efficacy of tropical forest restoration in recovering terrestrial small mammal communities, by combining measures of species diversity, composition, functional diversity and trait composition, in one of the world’s most irreplaceable protected areas, the Wet Tropics World Heritage Area of Australia. Specifically, this study examines: (1) whether small mammal species diversity increases with time since restoration; (2) whether functional diversity increases with restored forest age; and (3) whether restoration forests are converging in species composition and functional diversity on the ‘old-growth’ forest condition?

2.3 MATERIALS AND METHODS

2.3.1 Study area

The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-elevation (500-1000 m) plateau in north-east Queensland, Australia (approximately 17°- 17°30’ S, 145°30’- 145°45’ E). The climate is predominantly humid tropical with temperatures of 15.6°C – 25.3°C (Bureau of Meteorology 2016) and rainforests are mostly complex notophyll to mesophyll vine-forest (Stanton and Stanton 2005). Most rainforests on the Tableland were cleared for agriculture 80 - 100 years ago, although small patches of remnant rainforest remain, and large (>3,000 ha) tracts of unfragmented rainforest survive on steeper hillsides. In recent decades there has been an expansion of rainforest restoration projects, with a high diversity (10 - 100+ species) of native rainforest trees and shrubs planted at high densities (ca. 3000 - 6000 stems ha^{-1}), in small (<5 ha) patches and strips, mainly in riparian areas (Goosem and Tucker 2013). The resulting landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant rainforest, natural regrowth and replanted forests.

2.3.2 Study design

Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years (n=1). These restoration sites were categorised into young (1-5 years), mid-age (6-12 years) and old (13-17 years) restoration categories. All restoration sites were previously grazed pasture. Remnant rainforest patches were considered as the reference target sites, representing the desired end point of restoration (n=4) and ungrazed, abandoned (for between 3 and 10 years) pasture on previously cleared rainforest land as the reference degraded sites (n=4), representing the starting point of restoration. Sample sites were set up in four blocks within the landscape (Figure S2.7 in Supporting Information), with each block containing one site of each of the three restoration categories and starting and reference sites: pasture; young restoration planting; mid-age restoration planting; old restoration planting; and rainforest. Blocks were selected to represent the maximum variation in topographic, climatic and geological parameters in the landscape so all sites within a block were similar in these parameters. Sites were separated by >300 m and blocks by >1.5 km. All restoration and degraded pasture sites were of similar size and shape (1 – 4 ha) and were 200 – 1000 m from intact rainforest, connected through restored and remnant corridors. All rainforest reference sites were at least 300 ha in size. A 50m x 20m study plot was established in the centre of each site, within which all sampling took place.

2.3.3 Mammal trapping

To determine the structure of small/medium mammal assemblages at the sites, small-medium mammals were sampled over a consecutive three day/ three night period (Tasker and Dickman 2002) on four separate occasions at each site, covering both the wet (Feb-Mar 2014 and Feb-Mar 2015) and dry season (Sept-Oct 2013 and Sept-Oct 2014). Trapping occurred within a 50 m × 10 m transect at each site, and comprised six cage traps (30 x 30 x 60 cm; treadle wire-cage type; Mascot Wire Works, Enfield, New South Wales, Australia) and 20 baited Elliott A traps (10 × 10 × 30 cm aluminium box traps; Elliott type A, Elliot Scientific, Upwey, Victoria, Australia) baited with a mixture of oats, honey, vanilla essence, peanut butter, sardines and apple. Elliott traps were set in two parallel lines, at 5 m intervals along the outside edge of the transect. Wire cage traps were placed along the transect centre line at 0, 10, 20, 30, 40 and 50 m (Figure S2.8). The traps were placed 10 m apart as a compromise between maximising captures and working within the constraints of transect length and site size. Traps were checked in the morning between 0600 h and 1000 h. Each animal trapped was identified to species level, weighed, sexed, morphometrics measured and then released at the site of capture. All animals were tagged with a passive integrated transponder (PIT) tag (7 x 1.35 mm; Loligo Systems) to identify recaptures and avoid recounting individuals (Gibbons and Andrews 2004). The number of individuals caught at each site was used as an index of relative abundance of each species. Recaptures were not included. Total biomass was calculated as the total mass of all mammals captured at a site.

Rattus fuscipes and *R. leucopus*, two sympatric rat species in the study area, are difficult to distinguish without examining their skulls. Because all individuals could not be positively identified, records of these two species were combined in the analyses, following the protocol set by Williams et al. (2002), and are referred to as *R. fuscipes/leucopus*, although most individuals were likely to be *R. fuscipes* (Williams et al. 2002). *Melomys burtoni* and *M. cervinipes* are broadly sympatric in eastern Australia and are difficult to distinguish on external features. This study used two hind foot plantar pad measurements suggested by Frost (2009) and Van Dyck et al. (2013) to differentiate between the two *Melomys* species.

2.3.4 Measuring functional diversity

Species were characterised in terms of four main functional roles that were considered relevant to regenerating forests: feeding guild (herbivores; omnivores; folivores; insectivores; frugivores), foraging guild (terrestrials; fossorials [digging species]; scansorials; arboreals), diel activity (nocturnal or diurnal) (Van Dyck and Strahan 2008, Menkhorst and Knight 2011, Van Dyck et al. 2013) and mean body mass (Table S2.1; Appendix S 2.1). Statistical analyses were carried out using R version 3.1.1 (R Core Team 2014). Data from all four trapping rounds were pooled for analysis. The "FD" package for R was used to calculate four complementary measures of functional diversity which describe a different functional aspect of biological communities: (1) functional richness (FRic), is the range of functional roles in a community quantified by the volume of functional trait space occupied; (2) functional evenness (FEve), which summarizes how species' abundances are distributed throughout the occupied functional trait space; (3) functional divergence (FDiv), which describes the variation in the distribution of species abundances with respect to the centre of functional trait space (an abundance weighted centroid) (Villéger et al. 2008); and (4) functional dispersion (FDis), which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberté and Legendre 2010).

2.3.5 Data analysis

To estimate species richness in each habitat category and assess whether all mammal species had been sampled, sample-based species accumulation curves were generated, with 95% confidence intervals. The mean of four commonly used abundance based species richness estimators (ACE, CHAO1, JACK1 and Bootstrap) were also calculated, from 999 randomisations of observed species richness, using ESTIMATES v. 9.1.0 (Colwell 2013). Species diversity was measured using the Shannon-Wiener index and species evenness was calculated using Pielou's evenness index. Species richness was rarefied to the minimum number of individuals sampled in a site (n = 9 individuals).

To test for effects of restoration age and habitat category on mammal species diversity and composition, functional diversity and functional composition, generalised linear mixed effects models (glmm) were used with sampling block as a random effect. A contrast analysis was performed on the glmms with habitat category as a predictor, by obtaining confidence intervals using parametric bootstrapping, to determine whether the response variables differed between the habitat categories. Appropriate error structures were applied for all models (Table S2.2).

To assess whether restoration sites were progressing towards the reference sites in terms of species composition, a non-metric multidimensional scaling (NMDS) ordination analysis was used, using Bray-Curtis pairwise distances based on standardised, square root transformed abundance data. To test for differences in Bray-Curtis similarity to rainforest among habitat categories, a permutational multivariate analysis of variance (ADONIS) was performed. Glmms were used to explore the relationship between restoration age and Bray-Curtis similarity to rainforest and the total number of individuals of four different functional guilds: habitat specialisms; geographic range status; feeding guild; and foraging guild (see Table S2.1 for species classification).

2.4 RESULTS

2.4.1 Species diversity and composition

A total of 657 small-medium mammals from 12 species and 9 genera were recorded (excluding recaptures). Species accumulation curves revealed that sampling effort was adequate to characterise the local mammal community (Figure S2.9). The four common estimators of species richness suggest that between 74% of species in mid-restoration plantings to 99% in young restoration plantings were sampled (Table S3). The community attributes (abundance, total biomass, species richness, FRic, FEve, FDiv, FDis) across the experimental plots were not strongly correlated (Figure S2.10).

Total biomass (χ^2 = 10.62; P = 0.001; Figure 2.1c) and mean body mass (χ^2 = 12.95; P <0.001; Figure 2.1d) increased significantly with restoration age. However, observed species richness (χ^2 = 0.00; P = 0.997; Figure 2.1a), number of individuals (χ^2 = 0.038; P = 0.846; Figure 2.1b), estimated species richness (χ^2 = 0.01; P = 0.933; Fig. S5a), rarefied species richness (χ^2 = 0.13; P = 0.721; Figure S2.11b), Shannon-Wiener species diversity (χ^2 = 0.20; P = 0.655; Figure S2.11c) and Pielou's species evenness (χ^2 = 1.90; P = 0.168; Figure S2.11d) did not vary with restoration age. Number of individuals differed among habitat categories and was highest in pasture and lowest in mid restoration (χ^2 = 10.83; df = 4; P = 0.029; Figure 2.1f).

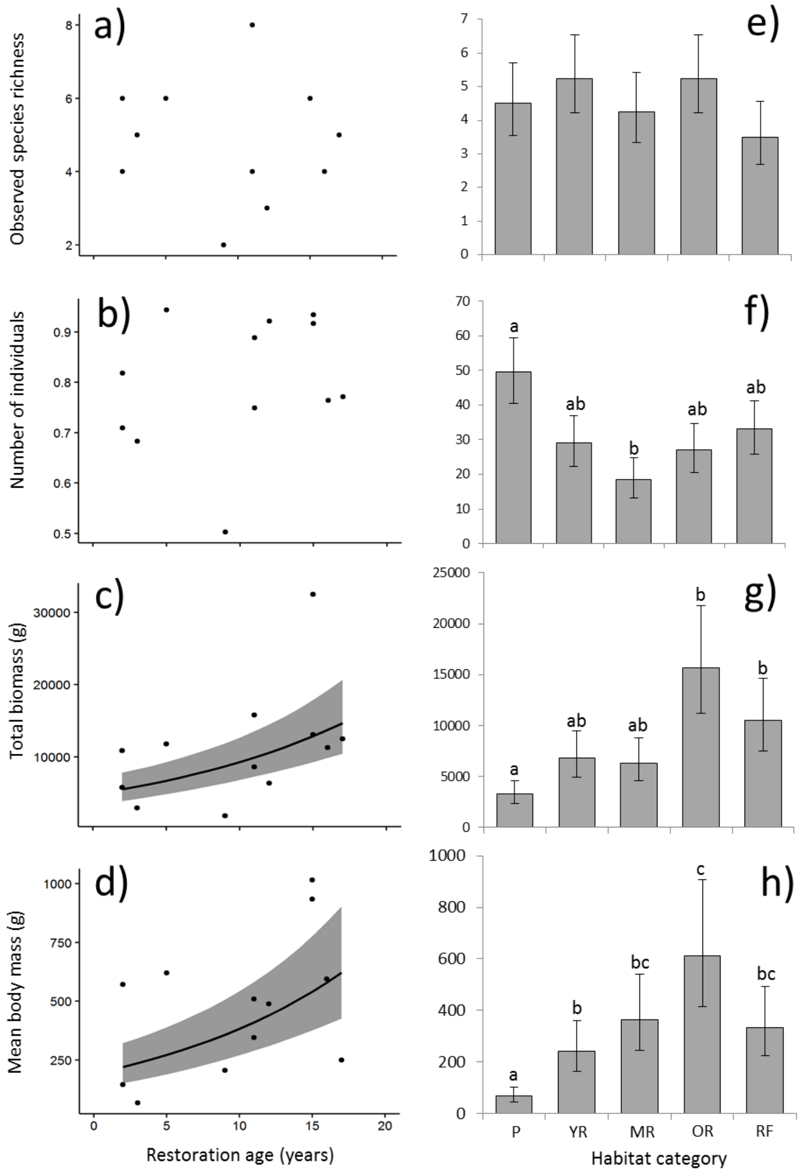

Figure 2.1 Relationship between restoration age and observed species richness, number of individuals, total biomass and mean body mass of small-medium mammals (a-d). Mean ± SE observed species richness, number of individuals, total biomass and mean body mass in the different habitat categories (e-h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

Total biomass (χ^2 = 16.16; df = 4; *P* = 0.003; Figure 2.1g) and mean body mass (χ^2 = 21.74; df = 4; *P* <0.001; Figure 2.1h) also differed among habitat categories and were largest in old restoration and lowest in pasture. Observed species richness (χ^2 = 1.8945; df = 4; *P* = 0.755; Figure 2.1e), estimated species richness (χ^2 = 1.95; df = 4 *P* = 0.744); Figure S2.11e, rarefied species richness (χ^2 = 5.07; df= 4; *P* = 0.281; Figure S2.11f), Shannon-Wiener species diversity (χ^2 = 3.84; df = 4; *P* = 0.429; Figure

S2.11g) and Pielou's species evenness (χ^2 = 0.71; df = 4 P = 0.950; Fig. Figure S2.11h) did not differ among habitat categories.

Species composition differed significantly among habitat categories (ADONIS: r^2 = 0.351, df = 4, P = 0.002; Figure 2.2). The NMDS ordination represented 85.6% of the assemblage dissimilarity and showed that the restoration sites are clearly progressing towards the rainforest reference sites (χ^2 = 7.33, P = 0.007; Figure 2.3b) and deviating from the pasture reference sites with increasing restoration age (χ^2 = 10.21, P = 0.001; Figure 2.3a; Figure 2.2). Bray-Curtis similarity to rainforest differed by habitat category (χ^2 = 10.42, df = 4, P = 0.034; Figure 2.3d), with the lowest value in pasture. Bray-Curtis similarity to pasture also differed among habitat categories (χ^2 = 65.48, df = 4, P < 0.001; Figure 2.3c), with the lowest values in mid-age and old restoration sites and rainforest.

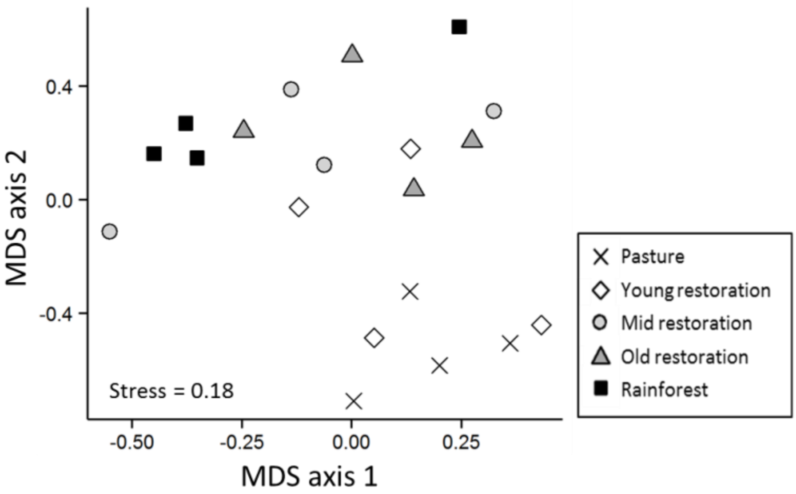

Figure 2.2 Non-metric multidimensional scaling (MDS) ordination of community assemblages of small-medium mammals among the different habitat categories (pasture; young restoration; mid restoration; old restoration; and rainforest) at the site scale, based on square-root transformed, standardised abundance data (r^2 = 0.86).

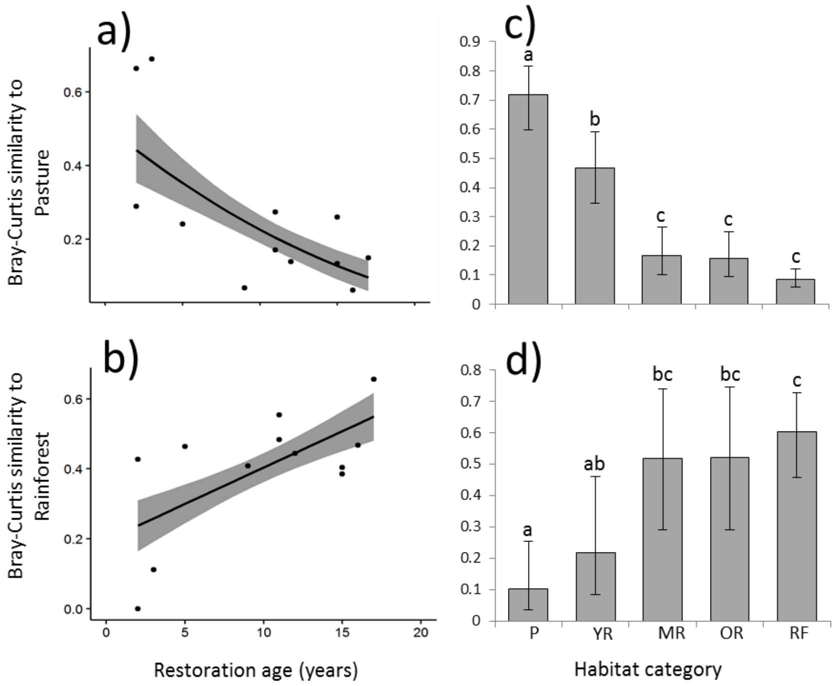

Figure 2.3 Relationship between restoration age and small-medium mammal assemblage similarity (Bray–Curtis index) to primary forest and pasture (a-b). Mean ± SE mammal assemblage similarity (Bray–Curtis index) to primary forest and pasture in the different habitat categories (c-d). P = pasture; YR= young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

2.4.2 Functional diversity

Functional richness did not vary with restoration age (χ^2 = 1.06, *P* = 0.303; Figure 2.4a) or habitat category (χ^2 = 1.35, df = 4, *P* = 0.557; Figure 2.4e). Functional evenness increased significantly with restoration age (χ^2 = 4.91, *P* = 0.027; Figure 2.4b) but only differed marginally among habitat categories (χ^2 = 6.34, df = 4, *P* = 0.175; Figure 2.4f), with the highest functional evenness in mid-restoration and the lowest in pasture and young restoration. Functional divergence did not vary by restoration age (χ^2 = 1.17, *P* = 0.279; Figure 2.4c) but differed significantly among habitat categories (χ^2 = 12.71, df = 4, *P* = 0.013; Figure 2.4g), with the lowest functional divergence in mid-restoration, and the highest in old restoration and rainforest. Restoration age increased functional dispersion (χ^2 =10.62, *P* = 0.001; Figure 2.4d), with the highest functional dispersion in old restoration and rainforest, and lowest in pasture (χ^2 = 8.24, df = 4, *P* = 0.083; Figure 2.4h).

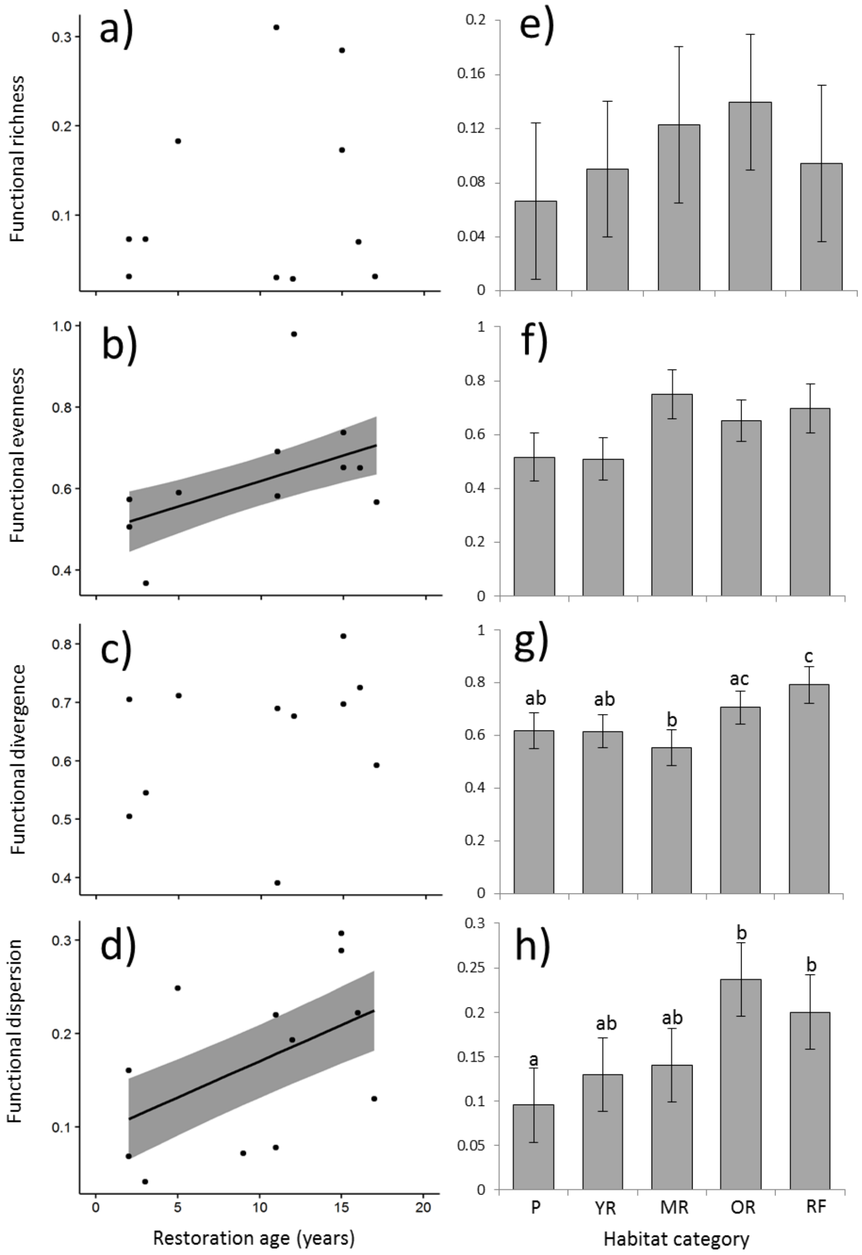

Figure 2.4 Relationship between restoration age and functional richness, functional evenness, functional divergence and functional dispersion of small-medium mammals (a-d). Mean ± SE functional richness, functional evenness, functional divergence and functional dispersion in the different habitat categories (e-h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

2.4.3 Functional composition and identity

In terms of habitat specialists and geographic range status, the abundance of open environment specialists ($\chi^2 = 12.59$, $P < 0.001$; Figure 2.5a) and invasive species ($\chi^2 = 18.49$, $P < 0.001$; Figure 2.5d) declined with restoration age, but the abundance of forest species ($\chi^2 = 7.97$, $P = 0.005$; Figure 2.5c) and Australian endemics ($\chi^2 = 11.45$,

$P < 0.001$; Figure 2.5f) increased. The abundance of habitat generalists ($\chi^2 = 0.00$, $P = 0.992$; Figure 2.5b) and Australian natives ($\chi^2 = 0.00$, $P = 0.996$; Figure 2.5e) did not vary with restoration age.

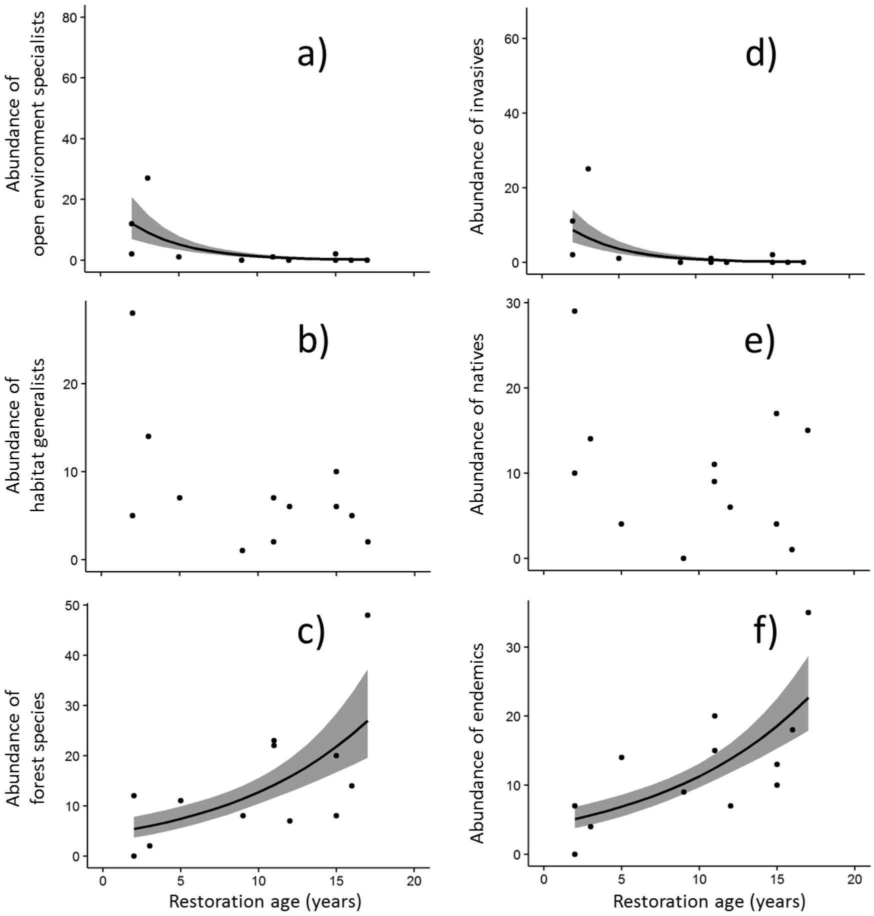

Figure 2.5 Relationship between restoration age and the total abundance of different functional guilds of small-medium mammals. Habitat specialisms: open environment specialists (a), habitat generalists (b) and forest species (c). Geographic range status: invasives (d), natives (e) and endemics (f).

In the feeding and foraging guilds, the abundance of herbivores ($\chi^2 = 8.85$, $P = 0.003$; Fig. 2.6e) and terrestrial foragers ($\chi^2 = 9.37$, $P = 0.002$; Fig. 2.6a) declined with restoration age, and increased for folivores ($\chi^2 = 6.01$, $P = 0.014$; Fig. 2.6g), arboreal foragers ($\chi^2 = 6.01$, $P = 0.014$; Fig. 2.6c). The abundance of omnivores ($\chi^2 = 0.14$, $P = 0.706$; Fig. 2.6f), scansorial foragers ($\chi^2 = 0.03$, $P = 0.852$; Fig. 2.6b) and fossorial foragers ($\chi^2 = 0.34$, $P = 0.562$; Fig. 2.6d) did not vary with restoration age.

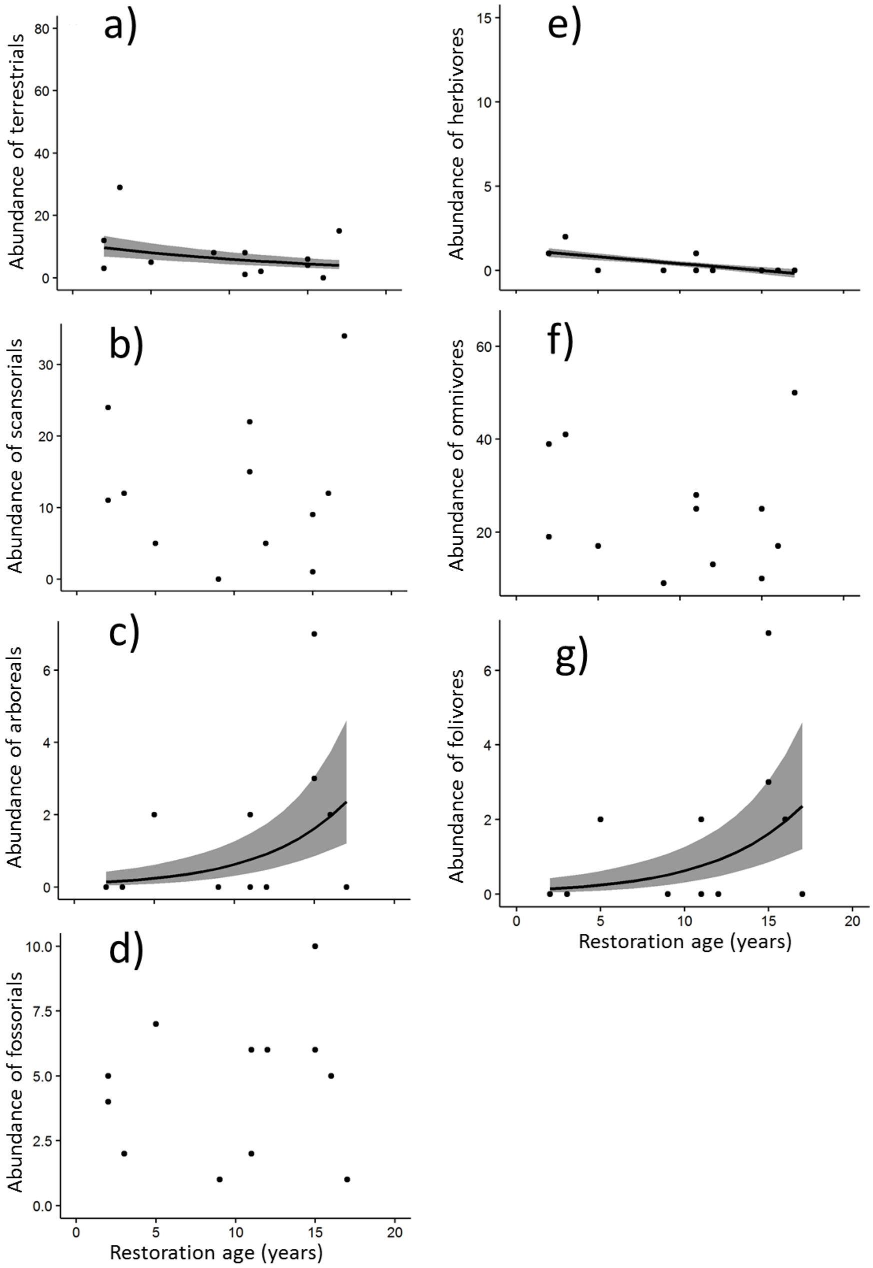

Fig. 2.6 Relationship between restoration age and the total abundance of different foraging guilds of small-medium mammals: Foraging guild: terrestrial foragers (a), scansorial foragers (b), arboreal foragers (c) and fossorial foragers (d). Feeding guild: herbivores (e), omnivores (f), and folivores (g).

2.5 DISCUSSION

The patterns in species and functional diversity recovery reported here demonstrate that reforestation can restore functionally diverse, rainforest-like mammal communities in a relatively short period of time, which may enhance the recovery of ecosystem functioning and thus ecosystem viability in recovering forests. This study also shows that traditional species-based metrics of diversity do not reveal the whole picture, and that by complementing these with measures of composition, functional diversity and functional identity, a better understanding of the efficacy of restoration practices is gained.

2.5.1 Species diversity and composition

Species richness, number of individuals and species diversity in the restored and reference rainforest sites were similar to or lower than in pasture sites. These results are commensurate with recent studies reporting similar species richness and abundance of small-medium mammals in restored habitats (including grasslands, riparian woodland strips and tropical rainforest) compared to reference remnant and degraded sites (Golet et al. 2011, Whitehead et al. 2014, Mérő et al. 2015). Although total species richness is the most frequently used measure of biodiversity recovery (Dunn 2004), Catterall et al. (2012) found that total bird species richness was a relatively insensitive measure of both forest–pasture differences and community development during tropical forest restoration in the study area. Here, this study found a marked increase in total biomass and mean body mass of mammals in the restored sites, indicating that as restoration sites age, they recover sufficient resources to support larger-bodied mammals. Increased total biomass and mean body mass in the older restoration sites may be related to higher levels of productivity.

Previous studies of species diversity patterns in mature and secondary tropical forests have shown that while secondary and recovering forests may harbour a similar number of species as mature forests (Dent and Wright 2009, Gibson et al. 2011), communities in secondary forests are usually dominated by different species to those in mature forest (Gardner et al. 2007, Edwards et al. 2011). Indeed, although restored sites had similar species richness to pasture sites in this study, they were progressing towards rainforest and deviating from pasture sites in terms of mammal composition (Figure 2.2 Figure 2.3). This confirms patterns found by similar studies on small-medium mammals (Whitehead et al. 2014), birds (Catterall et al. 2012), ants (Leach et al. 2013) and dung beetles (Derhé et al. 2016) in the study area.

A clear shift from pasture-like to more rainforest-like mammal communities approximately five years after planting is revealed here, which corresponds with the age at which canopy closure may start to occur (Goosem and Tucker 2013) and may be driven by canopy development (Neita and Escobar 2012). Indeed, small-medium mammal assemblage structure has been shown to be closely related to vegetation structure, particularly canopy cover (Williams et al. 2002).

2.5.2 Functional diversity

There was an increase in functional evenness (FEve) with restoration age (Figure 2.4b), consistent with previous studies of several taxa (Mouillot et al. 2013, Magnago et al. 2014) in which FEve declined with increasing disturbance levels. This increase in FEve with restoration age indicates that in older restoration sites, species are more evenly distributed along a gradient of ecosystem functions performed by those species and that dominant species differ in their contribution to the ecosystem functions. An increase in functional dispersion with restoration age (Figure 2.4d) was also found, i.e. a higher degree of niche differentiation, and thus low resource competition in the older restoration sites, suggesting that niche complementarity is enhancing species' occurrence probabilities and/ or abundances (Mason et al. 2013).

The functional metrics reveal that overall there is an increase in mammalian functional diversity as the restoration sites age; whereas the traditional species metrics failed to show a clear response with restoration age. Species richness measures do not reflect functional or ecological differences that determine species-specific response patterns, as well as the functional implications of species loss and recovery, and can therefore lead to misleading conclusions about trends in biodiversity (Dunn 2004, Mouillot et al. 2013, Derhé et al. 2016). These findings support previous meta-analyses showing that land use intensification and disturbance can reduce the functional diversity of mammal communities beyond changes in species richness alone (Flynn et al. 2009), potentially imperilling the provision of ecosystem processes and services. Moreover, it has been demonstrated that functional diversity responds differently to environmental, spatial and temporal processes compared to species abundance and biomass (da Silva and Hernández 2015). Functional diversity measures should therefore be used as a complementary tool to investigate species distribution and recovery, since they better explain the mechanistic link between organisms, ecosystem resource dynamics and the ecological processes that they govern (Mouillot et al. 2013, da Silva and Hernández 2015, Derhé et al. 2016).

2.5.3 Functional composition and identity

Although there were similar levels of functional richness in the restored and reference sites, the identity of the functional groups changed with restoration age. There was a clear shift in functional composition, from small-bodied, invasive, herbivorous, terrestrial open environment specialist species dominated communities in young restoration and pasture sites, to larger bodied, endemic, folivorous, arboreal, forest species dominated communities in the mid-age and old restoration sites. The shift from open environment specialist to forest species over the course of succession in these restored forests is consistent with patterns found when tropical forests have been able to regenerate naturally (Dent and Wright 2009).

Mammals are mediators of key ecosystem functions important to forest dynamics, including seed and spore dispersal and predation (Williams et al. 2000), nutrient cycling through dung deposition (Bardgett et al. 1998), and soil bioturbation (Fleming et al. 2014). These functions are particularly important for previously cleared forests that are known to have altered soil properties (Sahani and Behera 2001), which can strongly affect growth of tree seedlings, especially in their early stages (Tilman 1986). Mammals also contribute to nutrient recycling by returning organic matter and nutrients to the soil in relatively labile forms as dung and urine, which improves plant access to essential soil elements, including nitrogen, potassium and phosphorus (Loreau 1995) and may stimulate soil activity (Bardgett et al. 1998). The increased total biomass of mammals in older restored sites suggests that larger amounts of dung will be deposited in those sites, which may increase productivity (Williams and Haynes 1995) and have positive effects on seedling recruitment and forest regeneration.

Mammals also influence biological processes by the ingestion and movement of seeds and fungal spores. Australian native rodents (Forget and Vander Wall 2001) and marsupials (Dennis 2003) exhibit seed-caching behaviour, playing a critical role in dispersing plant seeds and influencing germination of plants involved (Midgley et al. 2002). Most mammals recorded in older restoration sites are species which are known to cache seeds and have been shown to increase germination rates, including the giant white tailed rat *Uromys caudimaculatus* (Theimer 2001), bush rat *Rattus fuscipes* and fawn footed melomys *Melomys cervinipes* (Elmouttie and Mather 2012), thus playing a significant role in enhancing seedling germination and growth in recovering forests.

2.5.4 Conservation implications

Species loss, like species recovery, follows a non-random pattern and is trait dependent (Larsen et al. 2005, Flynn et al. 2009). Disturbances can alter extinction order, and these non-random responses of communities to disturbances can have unexpectedly large ecological and functional consequences (Petchey and Gaston 2002, Larsen et al. 2005). Large body size is one of the most important global predictors of extinction risk in mammals (Cardillo et al. 2005, Hoffmann et al. 2011). The increase in total biomass and mean body mass with restoration age (Figure 2.1d) revealed in this study suggests that restoration sites may act as buffers for population declines of terrestrial mammals within the ‘critical weight range’ of between 100g and 5kg - those considered most at risk from extinction in Australia (Murphy and Davies 2014).

Since forest mammal species are relatively specialised and intolerant of the surrounding landscape matrix, this makes them more prone to extinction (Laurance 1991a, Turner 1996) and thus the recovery of forest mammal species in restored sites has positive conservation implications. The recovery of forest species in the restoration sites (Figure 2.5c) suggests that the habitat of restored sites is becoming structurally more similar to rainforest, since vegetation structure and habitat complexity have a strong influence on small mammal community structure (Williams et al. 2002).

The shift from abandoned pasture to established restored forests reported here represents a transition from invasive dominated degraded habitats (Figure 2.5d) to endemic dominated rainforest-like habitats (Figure 2.5f) in terms of mammal abundances. Indeed, the house mouse *Mus musculus*, listed as one of the world’s worst invasive alien mammal species (Lowe et al. 2000), was caught in high abundances in pasture and young restoration sites in this study. This shift will have further positive effects on biodiversity as invasive alien species are one of the key pressures driving biodiversity loss (Butchart et al. 2010).

2.6 SUPPORTING INFORMATION

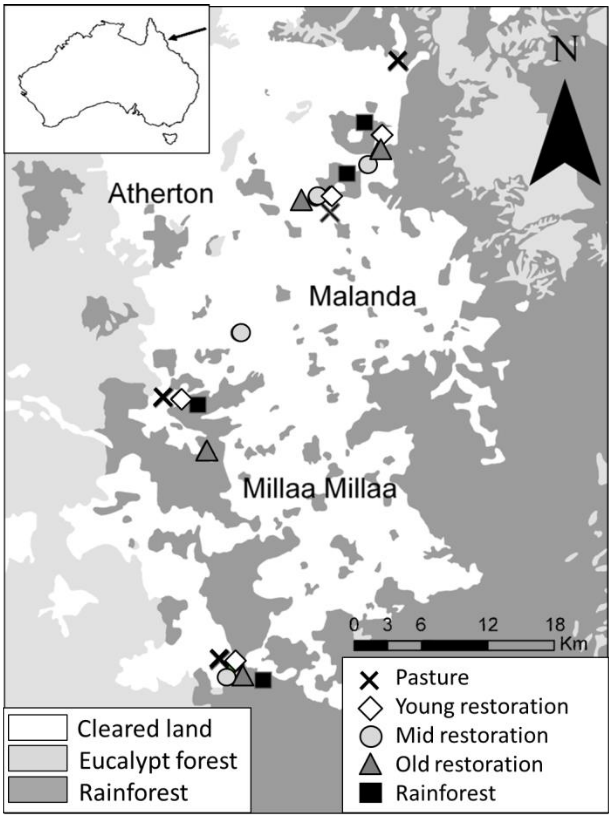

Figure S2.7 Map of the study area, showing the 20 study sites and areas of cleared forest, Eucalypt forest and rainforest. One 50m transect line was set up in each site comprising 20 Elliott traps and 6 wire cage traps.

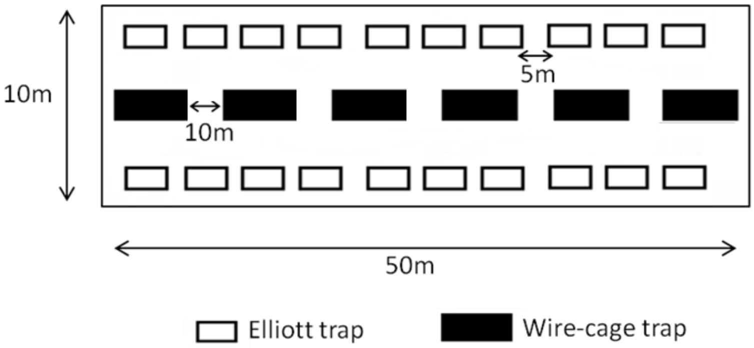

Figure S2.8 Mammal trapping grid showing location of baited Elliott and wire-cage traps along the 50m transect line at each site.

Table S2.1 Abundance of each mammal species and their assigned functional role values.

Species	**Abundance**	**Diel activity**	**Body mass (g)**	**Feeding guild**	**Foraging guild**	**Geographic range status***	**Habitat specialism***
Hypsiprymnodon moschatus	1	Diurnal	400	Frugivore	Terrestrial	Locally endemic	Forest species
Isoodon macrourus	36	Nocturnal	1000	Omnivore	Fossorial	Native	Habitat generalist
Melomys burtoni	75	Nocturnal	55	Omnivore	Terrestrial	Native	Habitat generalist
Melomys cervinipes	92	Nocturnal	55	Omnivore	Scansorial	Endemic	Forest species
Mus musculus	158	Nocturnal	10	Omnivore	Terrestrial	Invasive	Open environment specialist
Perameles nasuta	28	Nocturnal	1000	Omnivore	Fossorial	Endemic	Habitat generalist
Rattus fuscipes/ leucopus	123	Nocturnal	100	Omnivore	Terrestrial	Endemic	Forest species
Rattus lutreolus	2	Nocturnal	150	Herbivore	Terrestrial	Endemic	Open environment specialist
Rattus sordidus	38	Nocturnal	100	Herbivore	Terrestrial	Native	Open environment specialist
Sminthopsis murina	1	Nocturnal	30	Insectivore	Terrestrial	Endemic	Forest species
Trichosurus vulpecula	24	Nocturnal	2000	Folivore	Arboreal	Endemic	Forest species
Uromys caudimaculatus	79	Nocturnal	650	Omnivore	Scansorial	Native	Forest species

* Not used in the calculation of functional diversity metrics

Appendix S 2.1 Functional role assignment methods

To calculate functional diversity metrics, functional roles were given equal weighting and species were weighted by their relative abundance. Sample sites for which there were less than three species recorded (n=3) were excluded from any analysis involving the functional diversity metrics, because functional diversity indices cannot be calculated from less than three species.

Functional guild classification, diel activity and body mass

Information on species' feeding and foraging guilds, habitat specificity, geographic range status and diel activity was obtained from the literature (Dennis 2002, Dennis and Johnson 2008, Van Dyck and Strahan 2008, Menkhorst and Knight 2011, Van Dyck et al. 2013). Feeding guild relates to the food resource which the mammals are exploiting and was divided into five categories: herbivores (species which feed predominantly on grasses, grass seeds and grass stems); folivores (species which feed predominantly on leaves); frugivores (species which feed predominantly on fruits); insectivores (species which feed predominantly on invertebrates); and omnivores (species which feed on a variety of food).

Foraging guild relates to the foraging technique and was divided into four categories: terrestrial (species which forage predominantly on the ground); arboreal (species which forage predominantly in trees); scansorial (species that spend at least some of their time climbing); and fossorial (species which are adapted to, and predominantly forage by digging).

Habitat specificity was divided into three categories: open environment specialists (species which inhabit scrub, rank grass, anthropogenic habitats, cropland, open pasture and open woodlands); habitat generalists (species which tolerate a range of habitats, including disturbed areas, tall grassland, canefields, edges of rainforest, forested habitats with grassy understory open areas and suburban gardens); and forest species (species which are generally not found outside of wooded areas and inhabit closed wet sclerophyll and complex mesophyll vine forest, particularly where understorey is dense and tangled, as well as wet open woodland). To calculate mean body mass, each individual was weighed and the mean mass for each species was calculated.

Geographic range status relates to how restricted or endemic each species is to the study area, divided into four categories: invasive (species which are not native to Australia but which have become established); native (species which are native to Australia); endemic (species which are endemic to Australia); locally endemic (species which are *endemic* to the tropical rainforests of north-east *Queensland*).

Table S2.2 Structure of generalised linear mixed models for determining the effects of restoration age and habitat category on species, functional diversity and community metrics of small-medium mammals.

	Fixed effect: Restoration age			**Fixed effect: Habitat category**		
Response variable	**Random effect(s)**	**Error distribution**	**Transformation**	**Random effect(s)**	**Error distribution**	**Transformation**
Species metrics						
Species richness	Block	Poisson		Block	Poisson	
Abundance	Block	Negative binomial		Block	Gaussian	sqrt
Biomass	Block	Gamma (log link)		Block	Gaussian	$\log_{10}$
Species diversity	Block	Gaussian		Block	Gaussian	
Rarefied species richness	Block	Gaussian		Block	Gaussian	sqrt
Estimated species richness	Block	Negative binomial		Block	Gaussian	sqrt
Species evenness	Block	Gaussian		Block	Gaussian	
Functional diversity metrics						
Functional richness	Block	Gaussian		Block	Gaussian	
Functional evenness	Block	Gaussian		Block	Gaussian	
Functional divergence	Block	Gaussian		Block	Gaussian	
Functional dispersion	Block	Gaussian		Block	Gaussian	
Community metrics						
Bray-Curtis similarity to Pasture/ Rainforest	Block	Gaussian	sqrt	Block	Beta	
Mean body mass	Block	Gaussian	$\log_{10}$	Block	Gaussian	$\log_{10}$
Abundance of different habitat specialisms	Block	Negative binomial				
Abundance of different geographic range status	Block	Negative binomial				
Abundance of different feeding guilds	Block	Negative binomial				
Abundance of different foraging guilds	Block	Negative binomial				

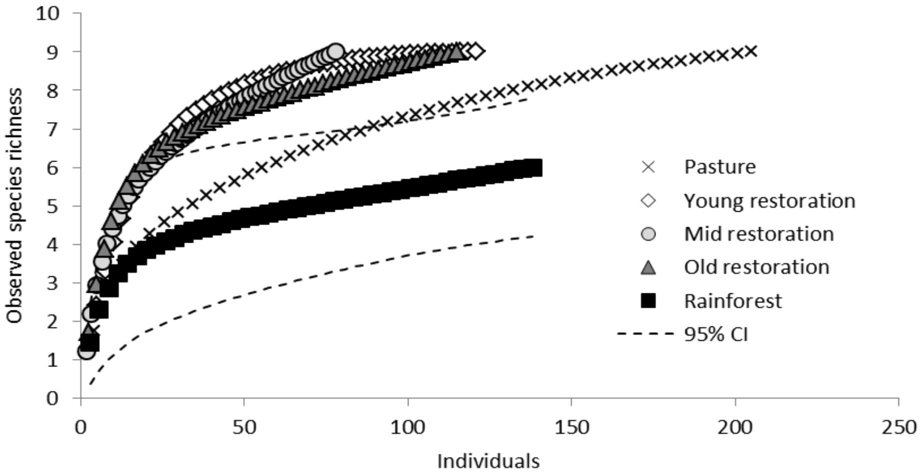

Figure S2.9 Observed species richness of small-medium mammals, constructed using sample-based rarefaction curves for the five habitat categories and scaled to show the number of individuals. Dashed line represents 95% confidence interval (CI) of rainforest.

Table S2.3 Summary of small-medium mammal community attributes: total abundance, observed (Sobs), estimated (Sest) and rarefied (Srar) species richness, proportion of species detected (Sobs / Sest), means species richness per sampling point (Sobs mean), species diversity measured using Shannon-Weiner diversity index, and species evenness measured using Pielou's index in each habitat category. Means (± 1 SE) are shown and superscripts represent pairwise differences at the $P \leq 0.05$ level.

Measure	**Pasture**	**Young restoration**	**Mid restoration**	**Old restoration**	**Rainforest**
Abundance	205^{a}	121^{ab}	78^{b}	115^{ab}	138^{ab}
Sobs	9^{a}	9^{a}	9^{a}	9^{a}	6^{a}
Sest	10.28^{a}	9.07^{a}	12.17^{a}	11.16^{a}	7.94^{a}
SRar	3.28^{a}	3.82^{a}	3.26^{a}	4.04^{a}	2.6^{a}
Sobs/ Sest	0.88^{a}	0.99^{a}	0.74^{a}	0.81^{a}	0.76^{a}
Sobs mean	1.75 ± 0.14^{a}	2 ± 0.16^{a}	3 ± 0.13^{a}	1 ± 0.15^{a}	3 ± 0.14^{a}
Species diversity	1.14 ± 0.24^{a}	1.31 ± 0.16^{a}	1.06 ± 0.31^{a}	1.4 ± 0.15^{a}	0.89 ± 0.09^{a}
Species evenness	0.79 ± 0.04^{a}	0.79 ± 0.06^{a}	0.78 ± 0.1^{a}	0.86 ± 0.05^{a}	0.79 ± 0.09^{a}

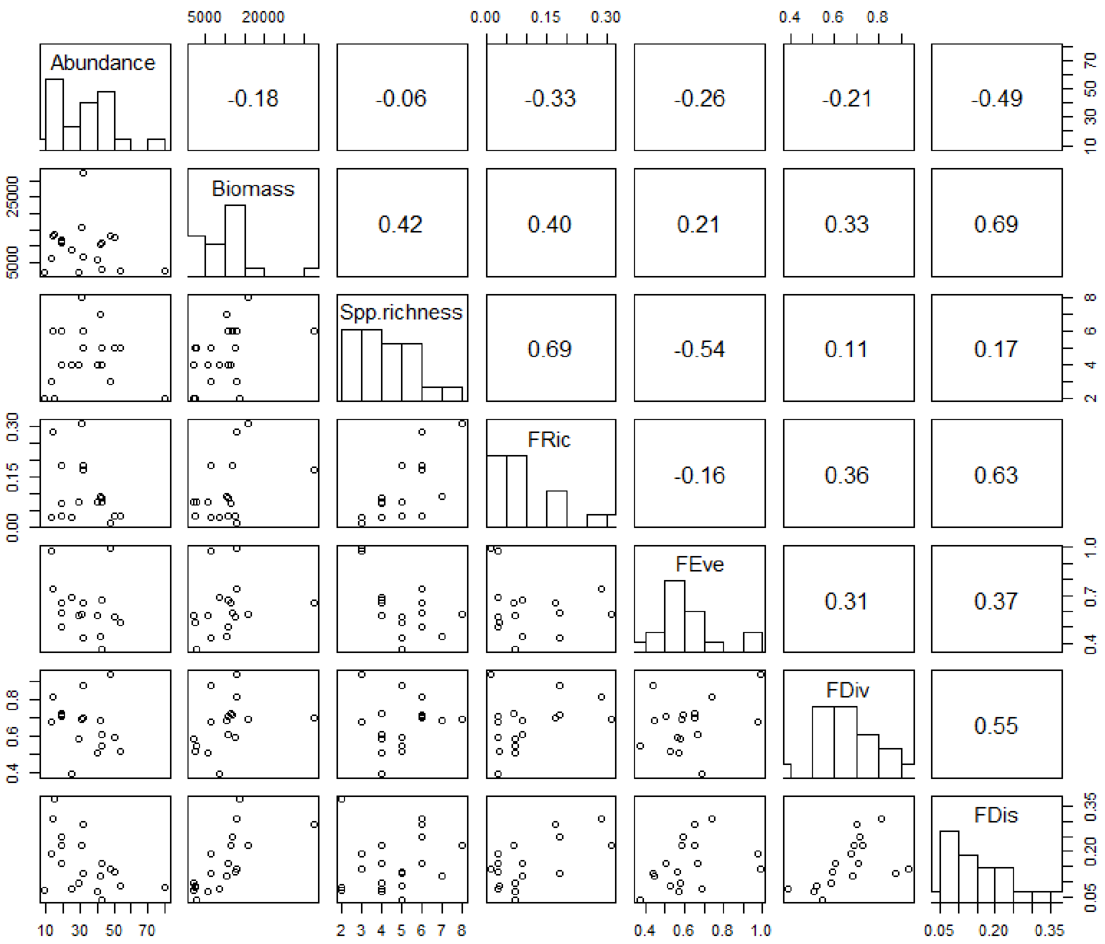

Figure S2.10 Associations between of small-medium mammal community attributes: bivariate plots (lower panels), distributions (diagonal), and Pearson’s ρ (upper panels).

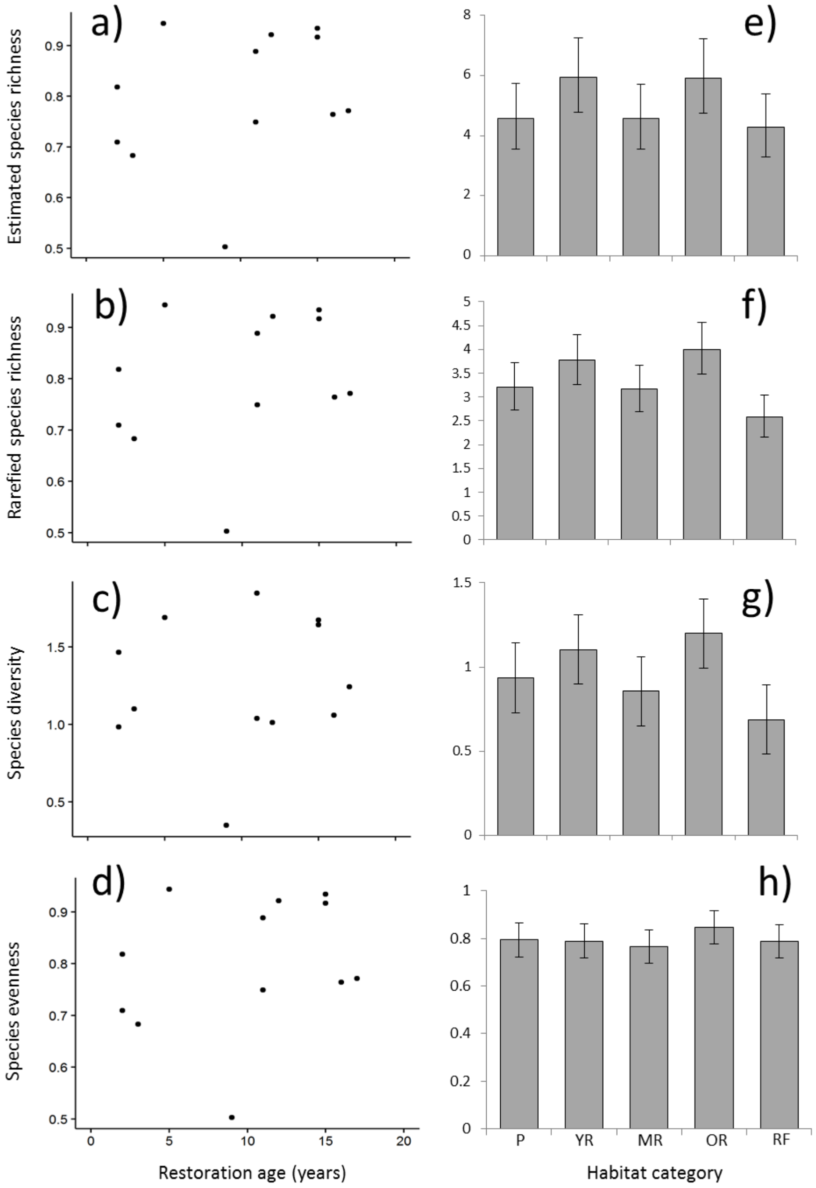

Figure S2.11 Relationship between restoration age and estimated species richness, rarefied species richness, Shannon- Wiener species diversity and Pileou's species evenness of small-medium mammals (a-d). Mean ± SE estimated species richness, rarefied species richness, Shannon- Wiener species diversity and Pileou's species evenness in the different habitat categories (ehj). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

Chapter 3

Measuring the success of reforestation for restoring dung beetle diversity and associated ecosystem functioning

Measuring the success of reforestation for restoring dung beetle diversity and ecosystem functioning

Publication status: Published in 2016 in the Journal of Applied Ecology (under the title: Measuring the success of reforestation for restoring biodiversity and ecosystem functioning)

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Author’s contribution:

Mia Derhé contributed to all aspects of the paper (designed and carried out all the experiments, performed all data analysis, interpreted all the data and wrote the manuscript). Helen Murphy provided advice on data analysis and comments on the manuscript. Geoff Monteith contributed to field work, beetle identification and provided comments on the manuscript. Rosa Menéndez contributed to the design of the experiment, assisted with field work, and provided advice on data analysis and comments on the manuscript.

3.1 SUMMARY

- Effective assessment of the success of ecological restoration projects is critical in justifying the use of restoration in natural resource management as well as improving best practice. One of the main goals of ecological restoration is the recovery of ecosystem function, yet most researchers assume that increasing species and or functional diversity equates with restoration of ecosystem function, rather than empirically demonstrating these mechanistic relationships.
- This study assesses how dung beetle species diversity, community composition, functional diversity and ecological functions vary along a restoration chronosequence and compare restored areas with reference (rainforest) and degraded (pasture) systems. The dung beetle diversity – ecosystem functioning relationship in the context of ecological rainforest restoration is investigated by testing the predictive power of traditional taxonomic indices and functional diversity metrics for functionality.
- Species richness, abundance, biomass and functional richness all increased with restoration age, with the oldest restoration sites being most similar to rainforest; whereas functional evenness and functional divergence decreased with restoration age. Community composition in the restored areas was clearly progressing towards the rainforest sites and deviating from the pasture sites with increasing restoration age.
- Secondary seed dispersal rates increased with restoration age, but there was only a weak positive relationship between dung removal and soil excavation and restoration age. Biodiversity metrics explained 47–74% of the variation in functions mediated by dung beetles; however, functional trait-based indices provided greater explanatory power of functionality than traditional species-based metrics.
- *Synthesis and Applications.* These results provide empirical evidence on the potential of tropical forest restoration to mitigate biodiversity losses, recovering not only faunal species diversity, but also functional diversity and ecosystem functions in a relatively short period of time. This study also demonstrates that functional trait-based metrics are better predictors of functionality than traditional species-based metrics, but that the relationship between restoration age, diversity

and ecosystem functioning is not straightforward and depends on the functions, traits and metrics used.

Key-words: dung beetles, ecological restoration, ecosystem function, functional diversity, functional traits, reforestation, Scarabaeinae, trait-based metrics, tropical forest, wet tropics

3.2 INTRODUCTION

Tropical forests provide significant local, regional and global human benefits through the provision of economic goods and ecosystem services, including storing more than half the world’s carbon (Pan et al. 2011). Despite this recognition, forest loss continues to increase, particularly in the tropics (Kim et al. 2015). Ecological restoration, both within and outside protected areas, is being increasingly applied worldwide and is regarded as a major strategy for reversing or mitigating tropical biodiversity losses and improving the provision of ecosystem services (Holl and Aide 2011). A popular method of ecological forest restoration is reforestation, which is the re-establishment of native tree cover to land previously cleared of rainforest (Lamb et al. 2005).

A combination of vegetation structure, faunal and floral species diversity/composition and ecosystem function have been suggested as a minimum set of attributes to assess the success of restoration projects (Ruiz-Jaen and Aide 2005, Wortley et al. 2013). However, whilst the trajectory of vegetation structure and diversity following restoration is relatively well understood, there has been limited research on faunal recovery (Majer 2009). Additionally, a key attribute set out by the Society for Ecological Restoration to determine when restoration has been accomplished, is that all functional groups necessary for the continued development and/or stability of the restored ecosystem are represented or have the potential to colonise (Shackelford et al. 2013).

Nonetheless, studies investigating the effect of restoration on functional diversity are few and far between. Recently, efforts have been made to bridge this gap: Audino et al. (2014) examined the response of dung beetle species diversity, composition and functional diversity to restoration of Atlantic forest in Brazil, showing that species composition but not functional diversity increased with restoration age. Despite these recent advances, there remains a distinct lack of research directly quantifying the recovery of ecosystem functioning alongside species and functional diversity recovery (Brudvig 2011, Montoya et al. 2012). Functional trait information and diversity indices complement traditional taxonomic based indices and when used together with assessments of ecological functions, can provide comprehensive evaluations of the success of restoration projects (Cadotte et al. 2011, Montoya et al. 2012). It is also valuable to quantify how restored diversity simultaneously influences a suite of ecosystem functions and whether the effect of diversity on multiple functions is different from its effect on individual functions.

This study aims to address this knowledge gap by directly measuring the response of dung beetle mediated ecosystem functions and dung beetle diversity to ecological restoration of tropical forests, and examines the mechanistic link between biodiversity recovery and functional recovery, using individual functions and an index of multifunctionality.

Dung beetles (Scarabaeidae: Scarabaeinae) are regarded as excellent bioindicators as they are diverse, taxonomically well-characterised, and are often considered a proxy for other taxonomic groups (Bicknell et al. 2014). They are particularly suitable for investigating the consequences of habitat recovery as they are stenotopic and thus intrinsically sensitive to alterations in environmental conditions (Nichols et al. 2007). Dung beetles are also mediators of key ecosystem functions important to forest dynamics, such as dung decomposition, secondary seed dispersal, soil bioturbation and nutrient cycling (Nichols et al. 2008). Tunnelling and dung burial by dung beetles relocates nutrient-rich organic material, instigates micro-organismal and chemical changes in the upper soil layers, aerates soils, improves water penetration and prevents nutrient loss (Brown et al. 2010). As dung beetles break down faecal matter and distribute it into the soil, they also relocate seeds from the point at which they were deposited through defecation by other animals (secondary seed dispersal), which increases seed survival (Andresen and Levey 2004, Nichols et al. 2008).

This study investigates the effect of tropical forest restoration on the recovery of taxonomic and functional diversity of dung beetles, and on the ecosystem functions they mediate, in one of the world’s most irreplaceable protected areas, the Wet Tropics World Heritage Area of Australia. To evaluate restoration success, a chronosequence approach of restored sites was used, as well as degraded and target reference systems, to examine patterns of dung beetle community assembly and functional recovery. In particular, this study examines: (1) whether increasing time since restoration leads to an increase in species diversity and a more rainforest-like community structure; (2) whether increasing time since restoration leads to an increase in functional diversity and functional efficiency; and (3) the relationship between biodiversity and ecosystem functioning in ecologically restored sites.

3.3 MATERIALS AND METHODS

3.3.1 Study area

The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-elevation (500-1000 m) plateau in north-east Queensland, Australia (approximately 17°- 17°30’ S, 145°30’- 145°45’ E). The climate is predominantly humid tropical with temperatures of 15.6°C – 25.3°C (Bureau of Meteorology 2016) and rainforests are mostly complex notophyll to mesophyll vine-forest (Stanton and Stanton 2005). Most rainforests on the Tableland were cleared for agriculture 80 - 100 years ago, although small patches of remnant rainforest remain, and large (>3,000 ha) tracts of unfragmented rainforest survive on steeper hillsides. In recent decades there has been an expansion of rainforest restoration projects, with a high diversity (10 - 100+ species) of native rainforest trees and shrubs planted at high densities (ca. 3000 - 6000 stems/ha), in small (<5 ha) patches and strips, mainly in riparian areas (Goosem and Tucker 2013). The resulting landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant rainforest, natural regrowth and replanted forests.

3.3.2 Study design

Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years (n=1). These restoration sites were categorised into young (1-5 years), mid-age (6-12 years) and old (13-17 years) restoration categories. All restoration sites were previously grazed pasture. Remnant rainforest patches were considered as the reference target sites, representing the desired end point of restoration (n=4) and ungrazed, abandoned (for between 3 and 10 years) pasture on previously cleared rainforest land as the reference degraded sites (n=4), representing the starting point of restoration. Sample sites were set up in four blocks within the landscape (Figure S3.6), with each block containing one site of each of the three restoration categories and starting and reference sites: pasture; young restoration planting; mid-age restoration planting; old restoration planting; and rainforest. Blocks were selected to represent the maximum variation in topographic, climatic and geological parameters in the landscape so all sites within a block were similar in these parameters. Sites were separated by >300 m and blocks by >1.5 km. All restoration and degraded pasture sites were of similar size and shape (1 – 4 ha) and were 200 – 1000 m from intact rainforest, connected through restored and remnant corridors. All rainforest reference sites were at least 300 ha in size. A 50m x 20m study plot was established in the centre of each site, within which all sampling took place.

3.3.3 Dung beetle community sampling

Sampling was conducted twice during the wet season: January - February and May - June 2014. In each site during each sampling period, four sampling points were placed 10 m apart along a linear transect. At each sampling point one standardised baited pitfall trap was installed (Spector and Forsyth 1998) filled with c. 100 ml of a 50:50 propylene glycol: water mixture and a few drops of detergent to sample dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Traps were baited alternately with agile wallaby (*Macropus agilis* [Gould]) dung and rotting mushrooms to attract a wider range of native species, as several species in the study area show specialisation to either mammalian dung or mushroom bait (Hill 1996). Traps were placed at a minimum of 20 m from the edge. Traps were opened in the morning between 07:00 and 10:00 and left in the field for 5 days. Beetles were identified to species level using voucher specimens and assisted by Geoff Monteith from the Queensland Museum. Voucher collections are lodged at the CSIRO Tropical Forest Research Centre in Atherton, Australia.

3.3.4 Dung beetle functions

Three dung beetle functions (dung removal, secondary seed dispersal and soil excavation) were measured using experimental dung baits set up in each site. Experiments were conducted during the wet season in January - February 2014 and were set up at least 4 days before dung beetle sampling took place. A small plot, c.30 cm in diameter, was established at each sampling point. In the centre of each plot, a 50 g ball of agile wallaby dung was placed (4 balls per site in total). Within each dung ball, 30 round plastic beads were placed, to act as seed mimics. Plastic seed mimics were used rather than real seeds to prevent possible seed predation (Slade et al. 2007). Seed mimics of 4 mm were used, since the majority of mammal-dispersed fleshy-fruited seeds in the study area are ≤4 mm (Westcott et al. 2008). The dung ball was surrounded by a wire mesh cylinder (grid size: 2 cm; height: 10 cm; diameter: 11 cm) with a plastic plate roof, allowing beetles to access the dung and avoiding interference by vertebrates. Dung balls were placed in the field between 07:00 and 10:00 and the remains were collected after 48 h. Any soil or dung beetles in the remaining dung were removed and all seed mimics present in the dung were removed and counted. The remaining dung was oven dried at 60°C until a constant weight was achieved. Dung ball controls (50 g wet mass; $n = 20$) were used to calculate the ratio of wet to dry dung mass and the mean dry mass of the control dung balls was taken as the starting dry mass for all experimental dung balls, enabling the amount of dung removed from each dung ball to be estimated. Loose soil around and beneath the experimental dung balls was collected and oven dried at 70°C until a constant weight was achieved, to determine the amount of soil excavated by dung beetles. It was assumed that plastic seed mimics absent from the dung remaining on the soil surface had been dispersed by dung beetles and so this was as the measure of seed dispersal.

3.3.5 Dung beetle functional traits

Five main functional traits that could directly influence the measured functions were examined: behavioural guild (tunnelers or rollers), diel activity (nocturnal or diurnal), body mass, diet preference (dung, mushroom or both) and diet breadth (number of bait types a species is attracted to). Details of functional trait determination are in Supporting Information (Table S3.1; Appendix S 3.1).

The “FD” package for R (R Core Team 2014) was used to calculate four complementary measures of functional diversity which describe a different functional aspect of biological communities: (1) functional richness (FRic), is the range of traits in a community quantified by the volume of functional trait space occupied; (2) functional evenness (FEve), which summarises how species’ abundances are distributed throughout the occupied functional trait space; (3) functional divergence (FDiv), which describes the variation in the distribution of species abundances with respect to the centre of functional trait space (an abundance weighted centroid) (Villéger et al. 2008); and (4) functional dispersion (FDis), which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberté and Legendre 2010).

3.3.6 Data analysis

Statistical analyses were carried out using R version 3.1.1 (R Core Team 2014). Data from both trapping rounds and from the four sampling points in each site were pooled, as these were not independent. To assess the completeness of this dung beetle survey for rainforest, pasture and each restoration category, sample-based species accumulation curves were generated, with 95% confidence intervals and the mean of four commonly used abundance based species richness estimators were also calculated (ACE, CHAO1, JACK1 and Bootstrap), from 999 randomisations of observed species richness, using ESTIMATES v. 9.1.0 (Colwell 2013).

For each site, observed and estimated species richness, species diversity (Shannon-Wiener index) and species evenness (Pielou’s evenness index) were calculated. To test for correlations amongst dung beetle functions, Pearson's product moment correlation coefficient was used. To test for effects of restoration age and habitat category on dung beetle species diversity and composition, functional diversity and ecosystem functions, generalised linear mixed effects models (glmm) were used with block as a random effect. The statistical significance of the predictor variable in each glmm was tested with analysis of variance (ANOVA). A contrast analysis was performed on the glmms, with habitat category as a predictor, by obtaining confidence intervals using parametric bootstrapping to determine whether the response variables differed among rainforest, pasture and restoration categories. Appropriate error structures were applied for all models (Table S3.2).

To assess whether restoration sites were progressing towards or diverging from the degraded and reference sites in terms of species composition, a non-metric multidimensional scaling (nMDS) ordination analysis was used based on Bray-Curtis pairwise distances using standardised and square root transformed abundance data. To test for differences in Bray-Curtis similarity to rainforest and pasture among restoration categories, a permutational multivariate analysis of variance (ADONIS) was used. Glmms were used to explore the relationship between restoration age and Bray-Curtis similarity to rainforest and pasture.

An information-theoretic approach was used to evaluate the relationships between relevant dung beetle community attributes (species richness, number of individuals, biomass, FRic, FEve, FDiv and FDis) and the three ecological functions. A multifunctionality variable was calculated (sensu Mouillot et al. 2011) as the mean value of the three functions (dung removal, soil excavation and seed dispersal) after standardising each function (mean of 0 and standard deviation of 1) in order to give them the same weight. Data from the first round of trapping only (Jan - Feb 2014) was used as this was conducted during the same time period as the functional manipulations. Outliers were identified using Cleveland dotplots, followed up with

Cook's Distance and removed from the analysis (n=1). Gaussian glmms were fitted to each of the relevant community attributes as well as null models (see Table S3 for model structures). The Akaike's Information Criterion corrected for small sample size (AIC_c) was used to evaluate models, by comparing the differences in AIC_c for each model with respect to the AIC_c of the best candidate model (Burnham and Anderson 2002). Based on the relative likelihoods of the different models, Akaike weights (w_i) were calculated to determine the weight of evidence in favour of each model being the best model in the set of candidate models, using the *MuMIn* package in R (Burnham and Anderson 2002).

3.4 RESULTS

3.4.1 Species richness, number of individuals, biomass and species diversity

A total of 3317 individuals from 39 dung beetle species in 8 genera were recorded (Table S3.1). Species accumulation curves suggest that sampling effort was adequate to characterise the local dung beetle community (Figure S3.7). The four common species richness estimators show that between 68% of species in old restoration plantings to 85% in rainforest were sampled (Table S3.4). The community attributes (number of individuals, observed species richness, total biomass, FRic, FEve, FDiv, FDis) across the experimental plots were uncorrelated, except for species richness and FRic, and biomass and FEve (Figure S3.8); however, because species richness is the most commonly used diversity index and biomass is known to have a significant effect on dung beetle functioning (Slade et al. 2011, Braga et al. 2013), these metrics were retained in the analyses.

Observed species richness (χ^2 = 11.77; P <0.001; Figure 3.1), estimated species richness (χ^2 = 9.80; P = 0.002; Fig. Figure 3.1b), number of individuals (χ^2 = 23.98; P <0.001; Figure 3.1c) and biomass (χ^2 = 6.49; P = 0.011; Figure 3.1d) all showed a significant positive relationship with restoration age. Shannon-Weiner species diversity (χ^2 = 3.64; P = 0.056; Figure 3.1e) and Pielou's species evenness (χ^2 = 0.40; P = 0.526) did not vary with restoration age. Observed species richness (χ^2 = 51.6; df = 4; P <0.001; Figure 3.1f), number of individuals (χ^2 = 91.10; df = 4; P <0.001; Figure 3.1h) and species diversity (Shannon index) (χ^2 = 22.31; df = 4; P <0.001; Figure 3.1j) were highest in rainforest and lowest in pasture and young restoration. Biomass (χ^2 = 91.10; df = 4; P <0.001; Figure 3.1i) and estimated species richness ($\chi^2 = 23.57$; df = 4; $P < 0.001$; Figure 3.1g) were lowest in pasture and young restoration, and highest in mid restoration, old restoration and rainforest. Species evenness did not differ among rainforest, pasture and restoration categories ($\chi^2 = 3.36$; df = 4; $P = 0.500$).

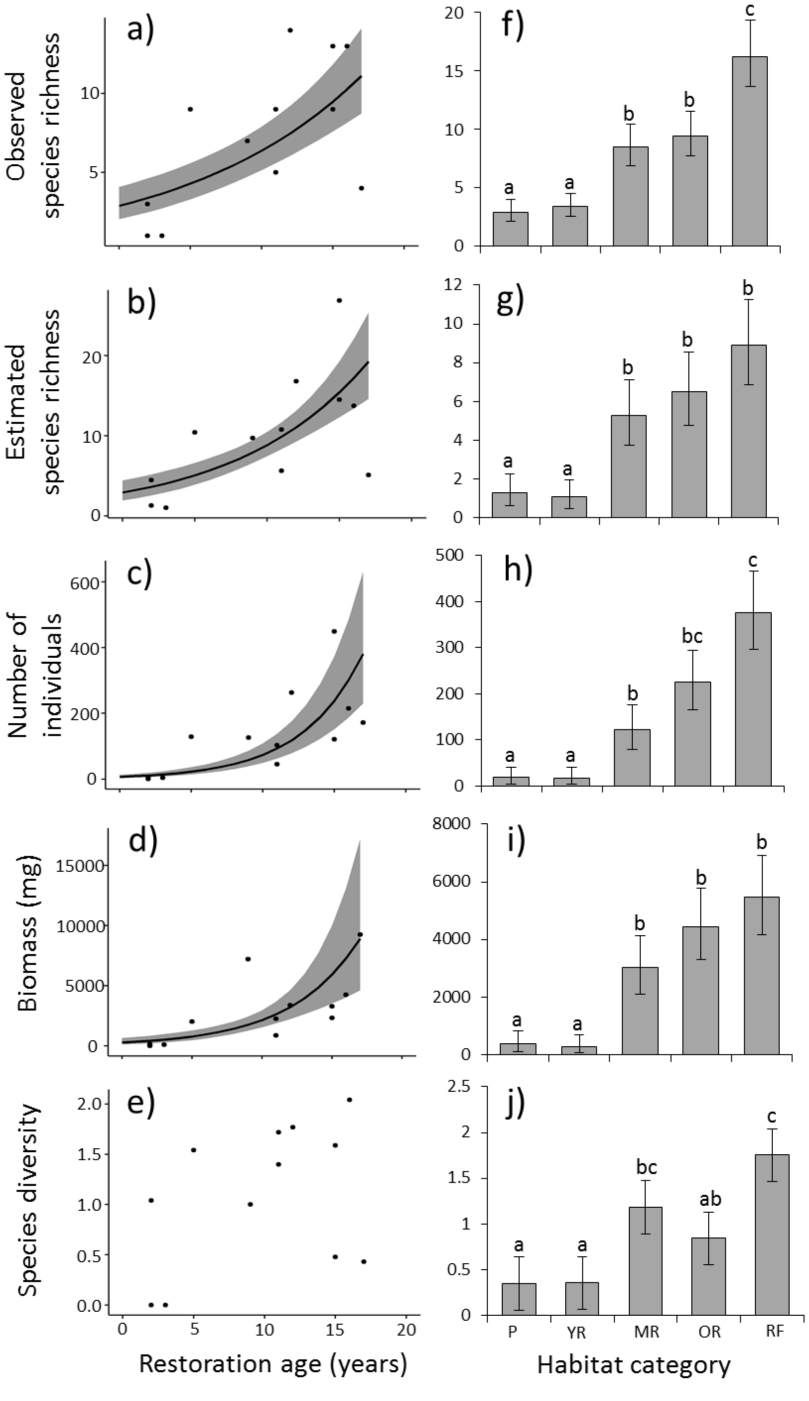


Figure 3.1 Relationship between restoration age and observed and estimated dung beetle species richness, number of individuals, biomass and species diversity (Shannon index) (a-e). Mean ± SE observed and estimated species richness, number of individuals, biomass and species diversity in the different habitat categories (f-j). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

3.4.2 Community composition

Species composition (Bray Curtis pairwise distances) differed significantly among rainforest, pasture and restoration categories (ADONIS: $r^2 = 0.36$, df = 4, $P = 0.003$; Figure 3.2; Table S3.5). The nMDS ordination represented 72.5% of the assemblage dissimilarity and showed that the restoration sites are clearly progressing towards the rainforest reference sites and deviating from the pasture reference sites with increasing restoration age (Figure 3.2). There was a significant positive relationship between restoration age and Bray Curtis similarity to rainforest ($\chi^2 = 8.03$; $P = 0.005$; Figure S3.9a), with the highest similarity value occurring in an old restoration site (0.511). Bray Curtis similarity to rainforest varied by restoration category ($\chi^2 = 34.38$; $P < 0.001$; Figure S3.9c), with the highest values in mid-stage and old restoration. Bray Curtis similarity to pasture did not vary with restoration age ($\chi^2 = 0.83$; $P = 0.363$; Figure S3.9b) or category ($\chi^2 = 0.83$; $P = 0.842$; Figure S3.9d).

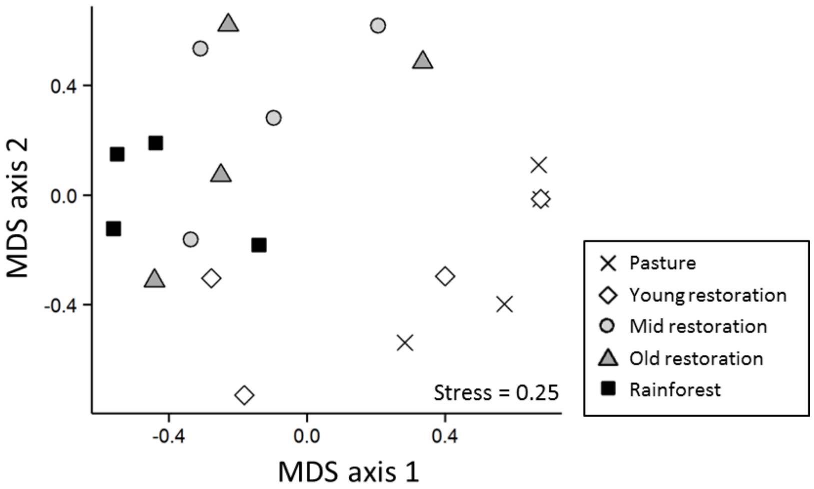


Figure 3.2 Non-metric multidimensional scaling (MDS) ordination of dung beetle community assemblages between the different habitat categories (pasture; young reforestation; mid reforestation; old reforestation; and rainforest) at the site scale, based on square-root transformed, standardised abundance data ($r^2 = 0.73$).

3.4.3 Functional diversity

Functional richness increased significantly with restoration age ($\chi^2 = 9.54$, $P = 0.002$; Figure 3.3a) and differed among rainforest, pasture and restoration categories ($\chi^2 = 32.11$, df = 4, $P < 0.001$; Figure 3.3e), with the highest functional richness in old restoration and rainforest and the lowest in pasture and young restoration. Restoration age had a negative effect on functional evenness ($\chi^2 = 8.42$, $P = 0.004$; Figure 3.3b) and functional divergence (χ^2 =6.61, P = 0.011; Figure 3.3c), but had no effect on functional dispersion (χ^2 = 1.65, P = 0.200; Figure 3.3d). Functional dispersion differed significantly among rainforest, pasture and restoration categories (χ^2 = 10.94, df = 4, P = 0.028; Figure 3.3h), with the highest values in rainforest. Neither functional evenness (χ^2 = 6.29, df = 4, P = 0.178; Figure 3.3f) or functional divergence (χ^2 = 2.50, df = 4, P = 0.644; Figure 3.3g) differed among rainforest, pasture and restoration categories.

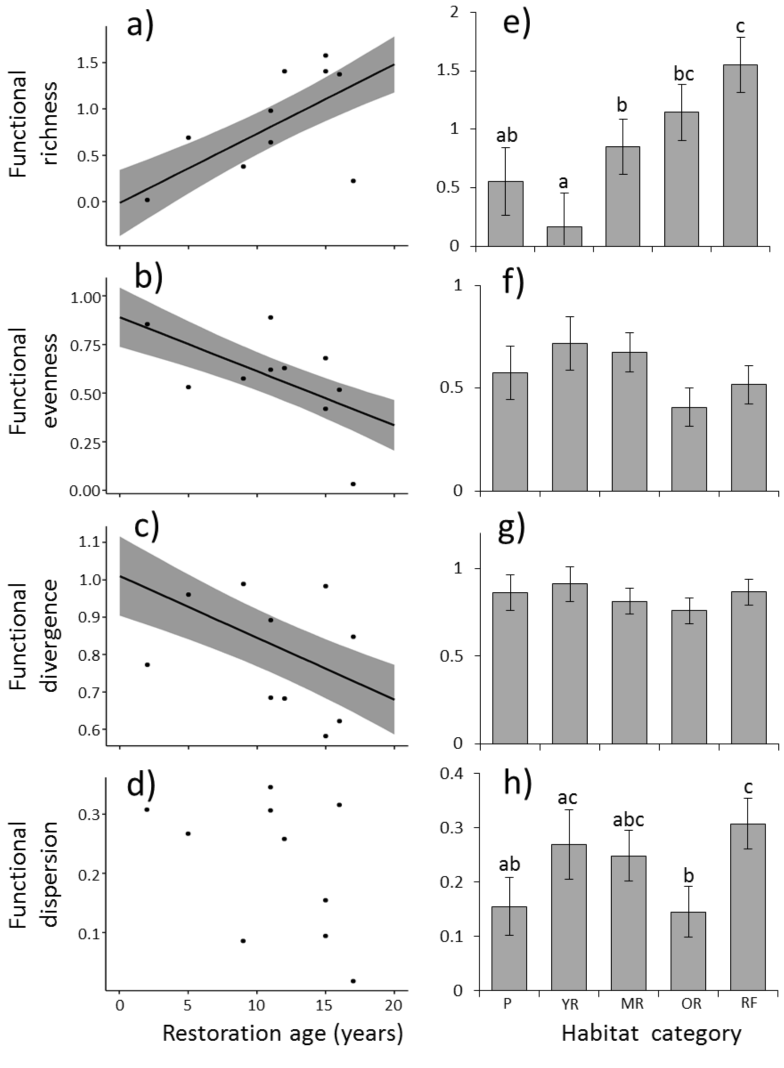


Figure 3.3 Relationship between restoration age and dung beetle functional richness, functional evenness, functional divergence and functional dispersion (a-d). Mean ± SE functional richness, functional evenness, functional divergence and functional dispersion in the different habitat categories (e-h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

3.4.4 Ecosystem functions

As expected, dung removal was positively correlated with both the amount of soil excavated (r = 0.73; p <0.001) and secondary seed dispersal (r = 0.95; p <0.001), as the former two functions are a direct consequence of the latter. Soil excavation was also positively correlated with seed dispersal (r = 0.81; p <0.001).

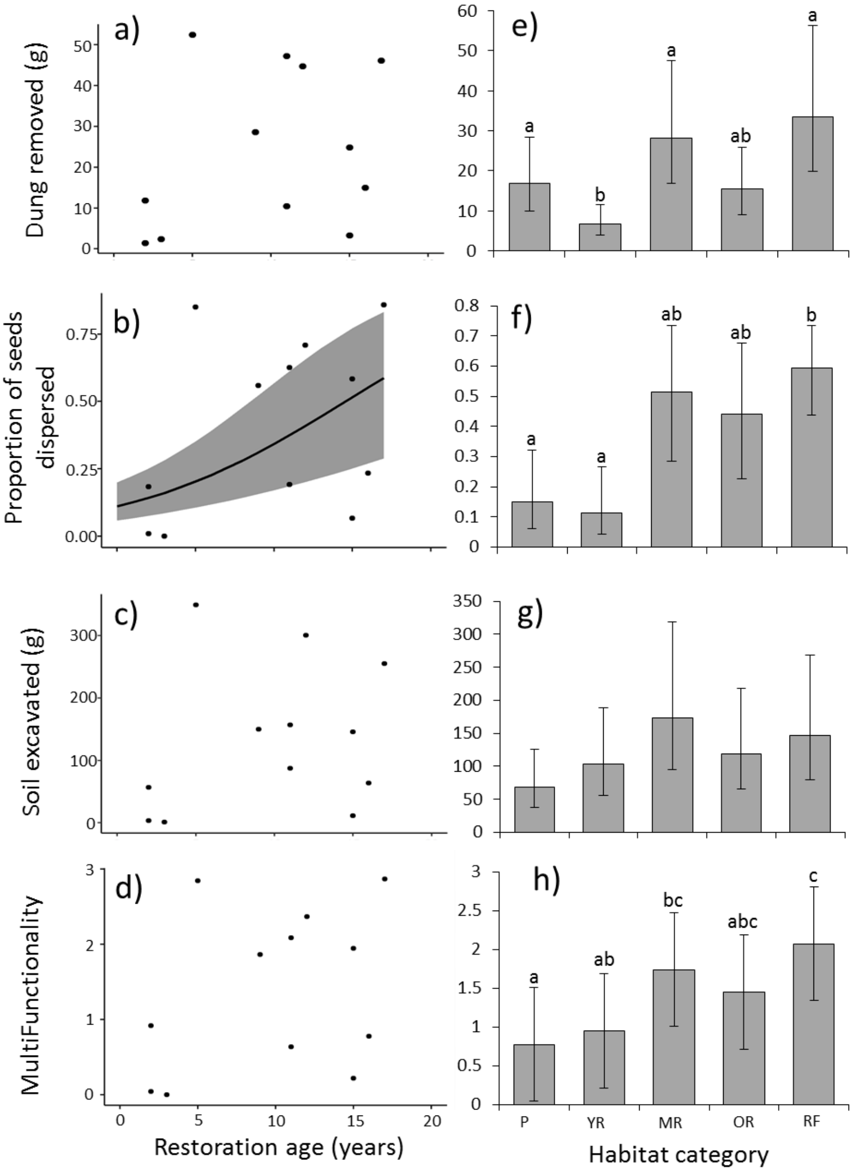


Figure 3.4 Relationship between restoration age and proportion of seeds dispersed, amount of dung removed, amount of soil excavated, and multifunctionality (a-d). Mean ± SE proportion of seeds dispersed, amount of dung removed, amount of soil excavated and multifunctionality in the different habitat categories (e-h). P= pasture; YR= young restoration; MR= mid-age restoration; OR= old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

Seed dispersal was positively influenced by restoration age (χ^2 = 5.46, *P* = 0.019; Figure 3.4b) and was highest in rainforest and the lowest in pasture and young restoration (χ^2 = 10.61, df = 4, *P* = 0.031; Figure 3.3f). There was no relationship between restoration age and dung removal (χ^2 = 2.85, *P* = 0.092; Figure 3.3a), soil excavation (χ^2 = 0.51, *P* = 0.477; Figure 3.3c) or multifunctionality (χ^2 = 1.36, *P* = 0.244; Figure 3.3d); however dung removal varied significantly among rainforest, pasture and restoration categories (χ^2 = 13.41, df = 4, *P* = 0.009; Figure 3.3e) with the lowest dung removal in young restoration. Multifunctionality was lowest in pasture and highest in rainforest (χ^2 = 9.72, df = 4, *P* = 0.045; Figure 3.3h). Soil excavation did not vary among rainforest, pasture and restoration categories (χ^2 = 1.37, df = 4, *P* = 0.849; Figure 3.3g).

3.4.5 Effect of diversity on dung beetle-mediated functions

The global models containing all biodiversity metrics and the random effect (‘block’; Table S3.6) explained 47-74% of the variation in functional efficiency (multifunctionality R^2 = 0.474; dung removal R^2 = 0.704; secondary seed dispersal R^2 = 0.738; soil excavation R^2 = 0.744). FDis, FDiv and FEve were the best predictors of multifunctionality, dung removal, seed dispersal and soil excavation (Table S3.6). However, there was very little difference in the strength of evidence between models including FDis, FDiv or FEve (Table S6), indicating that these three functional diversity metrics are the best predictors of dung beetle functionality, with FDis and FEve having a positive effect on multifunctionality, but FDiv having a negative effect (Figure 3.5).

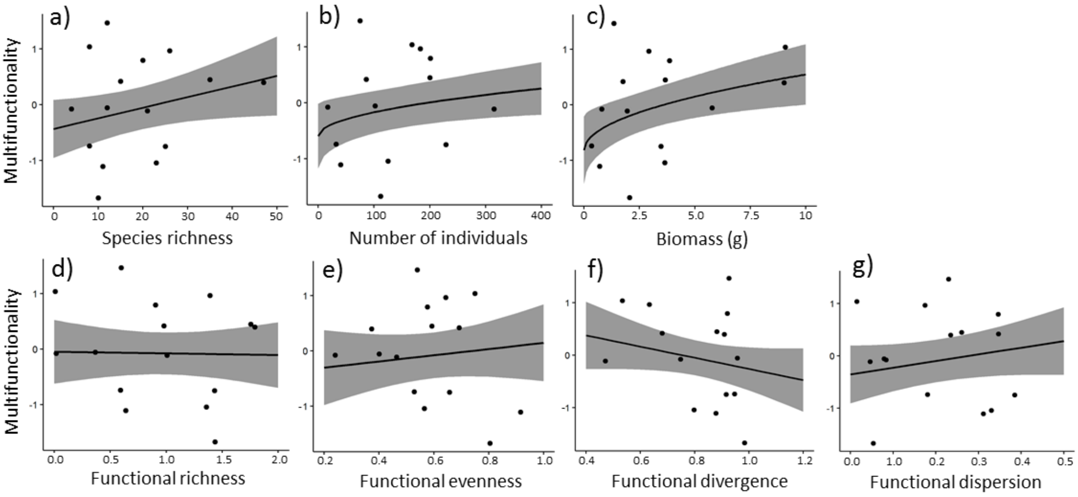


Figure 3.5 The effect of seven different dung beetle community attributes on multifunctionality (a-g). Models were generalised linear mixed effect models with Gaussian error distributions.

3.5 DISCUSSION

The patterns in species and functional recovery reported here show that restoration is an important strategy in mitigating biodiversity losses, reinstating functionality and recovering a degree of ecosystem stability. Functional trait-based metrics are revealed to better predictors of functionality than traditional species-based metrics. This study also reveals that the relationship between restoration age, diversity and ecosystem functioning is not straightforward and depends on the functions, traits and metrics used.

3.5.1 Species diversity and composition

There was a marked increase in species richness, number of individuals and biomass of dung beetles in the restored sites, in accordance with similar studies (Barnes et al. 2014, Hernandez et al. 2014). These patterns suggest that the carrying capacity of restored sites is higher than that of degraded pasture, but is still limited compared to rainforest. Restored sites were found to be progressing towards rainforest and deviating from pasture sites in terms of dung beetle community composition, with increasing restoration age (Figure 3.2; Figure S3.9), confirming patterns found by similar studies (Grimbacher and Catterall 2007, Audino et al. 2014). There was a clear shift from pasture-like to more rainforest-like dung beetle communities after around five years since planting, which corresponds with the age at which canopy closure occurs (Goosem and Tucker 2013) and may be driven by canopy development (Grimbacher and Catterall 2007). Indeed, vegetation structure is believed to be a main factor determining dung beetle community structure in tropical rainforests (Davis et al. 2002). The recovery of dung beetle communities in older restoration sites may also be partly due to an increase in colonisation opportunities as restoration sites get older.

Species diversity and evenness did not vary with restoration age, which is likely an artefact of the relatively high levels of species diversity and evenness in the mid-stage restoration sites. This may be caused by intermediate levels of disturbance in the mid-stage restoration sites (in that they are less disturbed than pasture and young restoration sites, but are not as established as old restoration sites). Disturbance strongly influences patterns of species diversity, resulting in maximum species diversity levels often occurring at intermediate levels of disturbance (Connell 1978).

3.5.2 Functional diversity

There was an increase in functional richness (FRic) with restoration age, supporting previous studies showing a negative relationship between FRic and habitat modification and disturbance (Barragán et al. 2011, Edwards et al. 2014). However, these findings contrast with those of Audino et al. (2014) who found that dung beetle FRic was lower in restored sites than in pasture. The discrepancies in these findings may be due to landscape context; functional trait (particularly body size) differences between Neotropical and Australian dung beetles; the presence of native grassland dung beetle species in the Neotropics (and the absence of such species in the Australian Wet Tropics); differences in community assembly patterns between the regions; differences in environmental factors; or differences in restoration techniques and management leading to slower functional diversity recovery in the Neotropical sites.

The increased FRic in restored sites indicates the recovery of forest species that fill vacant functional niches that are not present in the pasture sites. A greater range of functional traits in restored sites could represent complementarity of resource use, resulting in a higher amount of resources being used and thus stronger effects of diversity on ecosystem functioning (Díaz and Cabido 2001). Furthermore, greater functional richness increases the likelihood that some species will respond differently to variable conditions and perturbations (e.g. habitat disturbance, extreme climatic events) which contributes to the maintenance of long-term ecosystem functioning and increased ecosystem stability (Díaz and Cabido 2001). Contrary to expectations from studies reporting a decrease in functional evenness (FEve) with increasing disturbance levels (Gerisch et al. 2012, Mouillot et al. 2013), a decrease in FEve was found with restoration age in this study. Low FEve in restored sites indicates a concentration of species abundances along a small part of the functional trait gradient, i.e. the dominant species are similar in trait values, possibly indicating a high degree of habitat filtering (Mouchet et al. 2010). Pakeman (2011) suggests that low levels of FEve can be indicative of sites with little disturbance, where competition may be important in structuring the community, whereas in habitats where competition is low, such as highly disturbed areas, FEve can be high (even though FRic is low).

Functional divergence (FDiv) also decreased with restoration age, i.e. a low degree of niche differentiation, and thus high resource competition in the restoration sites indicating that further habitat filtering is occurring. FDis did not vary by site age and was slightly lower in old restoration than in mid stage restoration sites (as was the case for FEve and FDiv), which suggests that niche complementarity is not enhancing species occurrences (Mason et al. 2013), but that competition is the key driver of community structure in older restoration sites. Despite the potentially high levels of competition in older restoration sites indicated by slightly lower FEve and FDiv, the higher FRic and species richness at these sites suggests that older restoration sites contain more resources to enable competitive groups to co-exist.

3.5.3 Functional efficiency

Community attribute changes are somewhat mirrored by changes in ecological functions, as there was a positive relationship between secondary seed dispersal and restoration age and a weak positive relationship between dung removal and soil excavation and restoration age (non-significant). The increase in dung beetle mediated secondary seed dispersal in older restoration sites likely benefits seed survival and establishment (Nichols et al. 2007) which may have a positive impact on plant recruitment and successional recovery of restoration plantings. These findings are supported by previous studies reporting lower dung removal, dung decomposition and seed burial rates in disturbed and deforested habitats, compared with continuous, undisturbed forest (Horgan 2005, Braga et al. 2013). Nevertheless, ecological function recovery was slower than diversity recovery, which may be an artefact of the slightly elevated levels of functionality in mid-stage restoration sites. The higher levels of FDis (and less markedly, FEve) in young and mid-stage restoration sites are suggestive of more niche complementarity and less competition between functional groups. Thus in mid-stage restoration sites increased niche differentiation may be causing increased functioning.

3.5.4 Effect of diversity on dung beetle-mediated functions

Biodiversity metrics explained a fair amount (47-74 %) of the variation in functionality. Overall, traditional species-based diversity metrics had a positive relationship with functionality. However, functional trait-based indices provided greater explanatory power of functionality than species richness or abundance, and had an overall negative relationship with functionality. The best predictor of functionality was functional divergence (FDiv) which had a negative effect on functioning, implying that a dominance of one or a few similar traits were maximising functioning in the communities. This can happen when species are not equally important in their contributions to ecosystem processes, and a few key species with particularly important traits account for a large fraction of ecosystem functioning (Díaz and Cabido 2001). In particular, large-bodied tunnelers have been shown to make the largest contribution to functional efficiency and are generally better competitors (Slade et al. 2011, Nervo et al. 2014).

Two main hypotheses have been proposed to explain the role of diversity in ecosystem resource dynamics (Díaz and Cabido 2001, Loreau and Hector 2001). The ‘niche complementarity effect’ occurs when increasing diversity results in a greater range of functional traits (higher FRic), providing opportunities for more efficient resource use. Several studies have shown facilitatory effects in the interaction of dung beetle traits resulting in increased ecosystem functioning (Slade et al. 2007, Nervo et al. 2014, Menéndez et al. 2016). In contrast, the ‘selection effect’ occurs when increasing diversity results in a higher probability of the presence of species with particularly important traits, which can dominate ecosystem functioning, as is likely to be the case in this study, since functional divergence has a negative effect on functionality. The overall negative relationship between functional diversity metrics and functionality reported here demonstrates the complexity of biodiversity-functioning relationships and the variability in the predictive power of different species and functional trait metrics.

Functional trait-based metrics capture differences in species’ morphology, life-history traits and ecological niches which affect community responses to disturbance (Gerisch et al. 2012), and consequently changes to ecosystem function, extinction risk, and community reassembly processes. Furthermore, the mechanisms driving high functioning levels vary among the traits, functions and taxa considered (Gagic et al. 2015), as well as the environmental context (Steudel et al. 2012, Griffiths et al. 2014), and traditional taxonomic indices do not capture these complexities. As a consequence, traditional species diversity measures could potentially misjudge the true response of biodiversity and functioning to land-use change, disturbance and ecological restoration (Mouillot et al. 2013, da Silva and Hernández 2015). The idiosyncratic patterns between dung beetle-mediated function and diversity recovery demonstrate that the relationship between restoration age, taxonomic diversity, functional diversity and ecosystem functions is not always predictable and so inferences made about ecosystem functioning based on a taxonomic approach can be problematic. However, the greater explanatory power of functional diversity metrics to predict ecosystem functioning further highlights the importance of incorporating functional trait information and measures of ecological functions when assessing the effectiveness of ecological restoration.

3.6 DATA ACCESSIBILITY

Dung beetle community sampling and function data are available from the Dryad Digital Repository doi: 10.5061/dryad.63c7b.

3.7 SUPPORTING INFORMATION

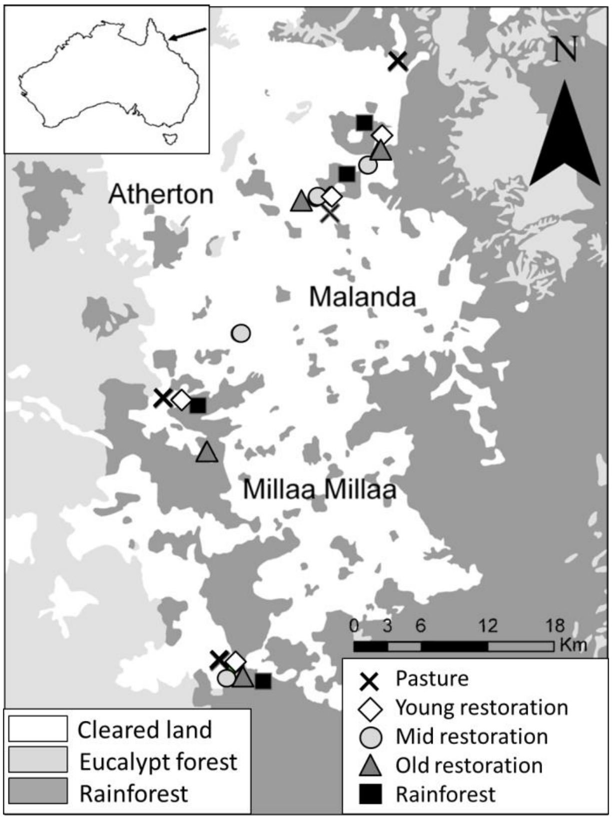


Figure S3.6 Map of the study area, showing the 20 study sites and areas of cleared forest, Eucalypt forest and rainforest. Each site comprised four sampling points (pitfall traps) for the measurement of community attributes and four experimental dung baits for the measurement of ecosystem functions.

Table S3.1 Abundance of each dung beetle species and their assigned functional trait values, including the habitat category within which the majority of individuals were recorded (‘habitat preference’): P= pasture; YR= young restoration; MR= mid-age restoration; OR= old restoration; RF = rainforest.

Species	**Taxonomic authority**	**Abundance**	**Body mass (mg)**	**Behavioural guild**	**Diel activity**	**Diet preference**	**Diet breadth**	**Habitat preference**
Amphistomus complanatus	Matthews (1974)	333	9.60	Rollers	Nocturnal	Dung	2	YR; MR; OR; RF
Amphistomus NQ3	NA	235	18.31	Rollers	Nocturnal	Dung	2	RF
Amphistomus NQ4	NA	18	3.21	Rollers	NA	Dung	2	OR; RF
Amphistomus NQ5	NA	302	1.55	Rollers	Nocturnal	Dung	2	OR; RF
Amphistomus pygmaeus	Matthews (1974)	7	3.30	Rollers	Nocturnal	Dung	1	RF
Aptenocanthon winyar	Storey & Monteith (2000)	4	9.00	Rollers	NA	Dung	1	RF
Boletoscapter cornutus	Matthews (1974)	68	8.50	Rollers	Nocturnal	Mushroom	1	MR; OR; RF
Coptodactyla depressa	Matthews (1976)	409	51.25	Tunnelers	Nocturnal	Both	2	MR; OR; RF
Coptodactyla onitoides	Matthews (1976)	79	76.80	Tunnelers	Nocturnal	Both	2	MR; OR
Demarziella interrupta	Matthews (1976)	27	2.95	Tunnelers	Nocturnal	Dung	2	P
Lepanus globulus	Matthews (1974)	11	4.43	Rollers	NA	Both	2	RF
Lepanus latheticus	Matthews (1974)	10	0.70	Rollers	NA	Mushroom	2	RF
Lepanus nitidus (large)	Matthews (1974)	13	3.50	Rollers	Diurnal	Both	2	RF
Lepanus nitidus (small)	Matthews (1974)	115	1.40	Rollers	Diurnal	Mushroom	2	RF
Lepanus NQ11	NA	1	0.70	Rollers	NA	NA	NA	OR
Lepanus NQ3	NA	3	0.75	Rollers	NA	Mushroom	2	RF
Lepanus NQ5	NA	1	0.87	Rollers	NA	Mushroom	NA	RF
Lepanus palumensis	Matthews (1974)	1	0.80	Rollers	NA	Mushroom	1	RF
Lepanus villosus	Matthews (1974)	12	0.65	Rollers	Diurnal	Mushroom	1	RF
Onthophagus bornemisszanus	Matthews (1972)	2	20.00	Tunnelers	NA	NA	NA	P
Onthophagus bundara	Storey & Weir (1990)	1	1.29	Tunnelers	NA	NA	NA	RF
Onthophagus capelliformis	Matthews (1972)	113	25.47	Tunnelers	Nocturnal	Dung	1	YR; MR; OR; RF

Onthophagus capella	Matthews (1972)	17	52.95	Tunnelers	Nocturnal	Dung	1	P; YR
Onthophagus cuniculus	Matthews (1972)	31	19.70	Tunnelers	Diurnal	Mushroom	2	P; YR
Onthophagus darlingtoni	Matthews (1972)	3	15.62	Tunnelers	Nocturnal	Dung	2	RF
Onthophagus dicranocerus	Matthews (1972)	18	31.04	Tunnelers	Nocturnal	Dung	1	MR; OR; RF
Onthophagus gulmarri	Matthews (1972)	4	9.00	Tunnelers	Nocturnal	Dung	1	MR; RF
Onthophagus millamilla	Matthews (1972)	59	4.38	Tunnelers	Diurnal	Dung	2	MR; OR; RF
Onthophagus mundill	Matthews (1972)	1	61.00	Tunnelers	Nocturnal	NA	NA	RF
Onthophagus nigriventris	D'Orbigny (1902)	2	38.31	Tunnelers	Diurnal	NA	NA	OR
Onthophagus paluma	Matthews (1972)	1	28.50	Tunnelers	Diurnal	Dung	1	P
Onthophagus rubicundulus	Matthews (1972)	15	1.86	Tunnelers	Diurnal	Dung	2	RF
Onthophagus semimetallicus	Matthews (1972)	12	12.0	Tunnelers	Nocturnal	Dung	1	MR
Onthophagus wagamen	Matthews (1972)	62	5.70	Tunnelers	Diurnal	Dung	1	RF
Onthophagus waminda	Matthews (1972)	84	1.93	Tunnelers	Diurnal	Dung	1	YR; MR; OR; RF
Onthophagus yungaburra	Matthews (1972)	136	2.57	Tunnelers	Diurnal	Dung	1	RF
Temnoplectron aeneopiceum	Matthews (1974)	1	4.56	Rollers	Nocturnal	Unknown	1	RF
Temnoplectron bornemisszai	Matthews (1974)	18	63.50	Rollers	Nocturnal	Dung	2	RF
Temnoplectron politulum	Matthews (1974)	387	18.56	Rollers	Nocturnal	Both	2	OR; RF

Appendix S 3.1 Functional trait assignment methods

Where information on a species was unavailable, NAs were used. This was necessary for eight species for diet preference and breadth, and for ten species for diel activity and behavioural guild. In order to calculate functional diversity metrics, traits were given equal weighting and species were weighted by their relative abundance. Sample sites for which there were less than three species recorded (n=4) were excluded from any analysis involving the functional diversity metrics, because functional diversity indices cannot be calculated from less than three species.

Behavioural guild, diel activity and body mass

Information on species' behavioural guilds and diel activity was obtained from the literature (Matthews 1972, 1974, 1976, Storey and Weir 1989, Storey and Monteith 2000) and from observations conducted by the authors (MD, GM and RM). Dung beetles were classified according to their resource relocation behaviour into either tunnelers, which bury dung directly beneath the dung pile; and rollers, which transport and bury dung some distance away from the dung pile (Hanski and Cambefort 1991). To calculate body mass, 1-20 specimens (unknown sex) of each species were dried in a forced draught oven at 60°C to a constant weight, and weighed using a 0.0001 g precision balance.

Diet preference and breadth

Diet preference was investigated using traps alternately baited with wallaby dung (n = 80 traps) and mushrooms (n = 80 traps). Trap design was identical for traps baited with both bait types. I used the proportion of individuals of each species attracted to a certain bait to determine bait specificity. Species of which >80% individuals were recorded in traps baited with dung were categorised as 'dung specialists'; species of which >80% individuals were recorded in traps baited with mushroom were categorised as 'mushroom specialists'; and species of which 25-75% individuals were recorded in traps baited with dung were categorised as 'diet generalists'. Diet breadth was calculated as the number of bait types that a species was attracted to (species caught in both dung and mushroom baited traps = 2; species caught only in either dung or mushroom = 1). The minimum number of individuals of each species required to calculate diet preference and breadth was n = 3. Information on diet preference and breadth has implications for resource partitioning between functional groups.

Table S3.2 Structure of generalised linear mixed models for determining the effects of restoration age and habitat category on species, functional diversity and community metrics and ecological functions of dung beetles.

	Fixed effect: Restoration age			**Fixed effect: Habitat category**		
Response variable	**Random effect(s)**	**Error distribution**	**Transformation**	**Random effect(s)**	**Error distribution**	**Transformation**
Species metrics						
Species richness	Block	Poisson		Block	Poisson	
Abundance	Block	Negative binomial		Block	Negative binomial	
Biomass	Block	Gamma (log link)		Block	Gaussian	$\log_{10}$
Species diversity	Block	Gaussian		Block	Gaussian	
Rarefied species richness	Block	Gaussian	sqrt	Block	Gaussian	sqrt
Estimated species richness	Block	Negative binomial		Block	Gaussian	sqrt
Species evenness	Block	Gaussian		Block	Gaussian	
Functional diversity metrics						
Functional richness	Block	Gaussian		Block	Gaussian	
Functional evenness	Block	Gaussian		Block	Gaussian	
Functional divergence	Block	Gaussian		Block	Gaussian	
Functional dispersion	Block	Gaussian		Block	Gaussian	
Community metrics						
Bray-Curtis similarity to Pasture/ Rainforest	Block	Beta		Block	Beta	
Ecological functions						
Dung removal	Block	Gaussian	$\log_{10}$	Block	Gaussian	$\log_{10}$
Seed dispersal	Block	Beta		Block	Beta	
Soil excavation	Block	Gamma (log link)		Block	Gamma (log link)	
Multifunctionality	Block	Gaussian		Block	Gaussian	

Table S3.3 Structure of global models for determining the effects of dung beetle species richness (SpRic), abundance (Abun), biomass (Biom), functional richness (FRic), functional evenness (FEve), functional dispersion (FDis) and functional divergence (FDiv) on dung removal (Dung), seeds dispersal (Seeds), soil excavation (Soil) and multifunctionality (Multi).

Global model	**Model**	**Random effect(s)**
log(Dung) ~ SpRic + sqrt(Abun) + sqrt(Biom) + FRic + FEve + FDis + FDiv	lmm	Block
log(Seeds) ~ SpRic + sqrt(Abun) + sqrt(Biom) + FRic + FEve + FDis + FDiv	lmm	Block
log(Soil) ~ SpRic + sqrt(Abun) + sqrt(Biom) + FRic + FEve + FDis + FDiv	lmm	Block
Multi ~ SpRic + Abun + Biom + FRic + FEve + FDis + FDiv	lmm	Block

*Number of individuals (abundance) and biomass were square root transformed to satisfy assumptions of normality

Table S3.4 Summary of dung beetle community attributes: total abundance, observed (Sobs) and estimated (Sest) species richness, and proportion of species detected (Sobs / Sest) in each habitat category. Superscripts represent pairwise differences at the $P \leq 0.05$ level.

Measure	**Pasture**	**Young restoration**	**Mid restoration**	**Old restoration**	**Rainforest**
Abundance	78^{a}	138^{a}	537^{b}	957^{bc}	1607^{c}
Sobs	7^{a}	11^{a}	20^{b}	22^{b}	32^{c}
Sest	8.97^{a}	13.56^{a}	28.20^{b}	32.48^{b}	37.70^{b}
Sobs/ Sest	0.78^{a}	0.81^{a}	0.71^{a}	0.68^{a}	0.85^{a}

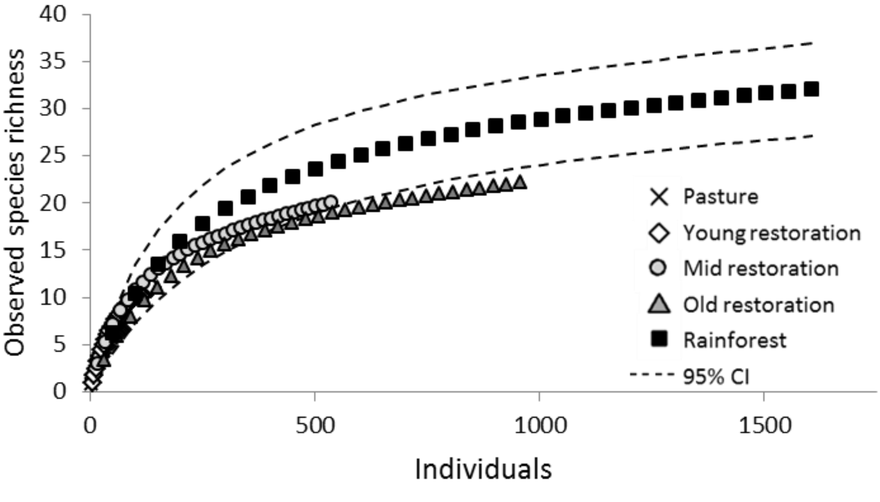


Figure S3.7 Dung beetle species accumulation curves constructed using sample-based rarefaction curves for pasture, rainforest and the three restoration categories (scaled to show the number of individuals). Dashed line represents 95% confidence interval (CI) of rainforest.

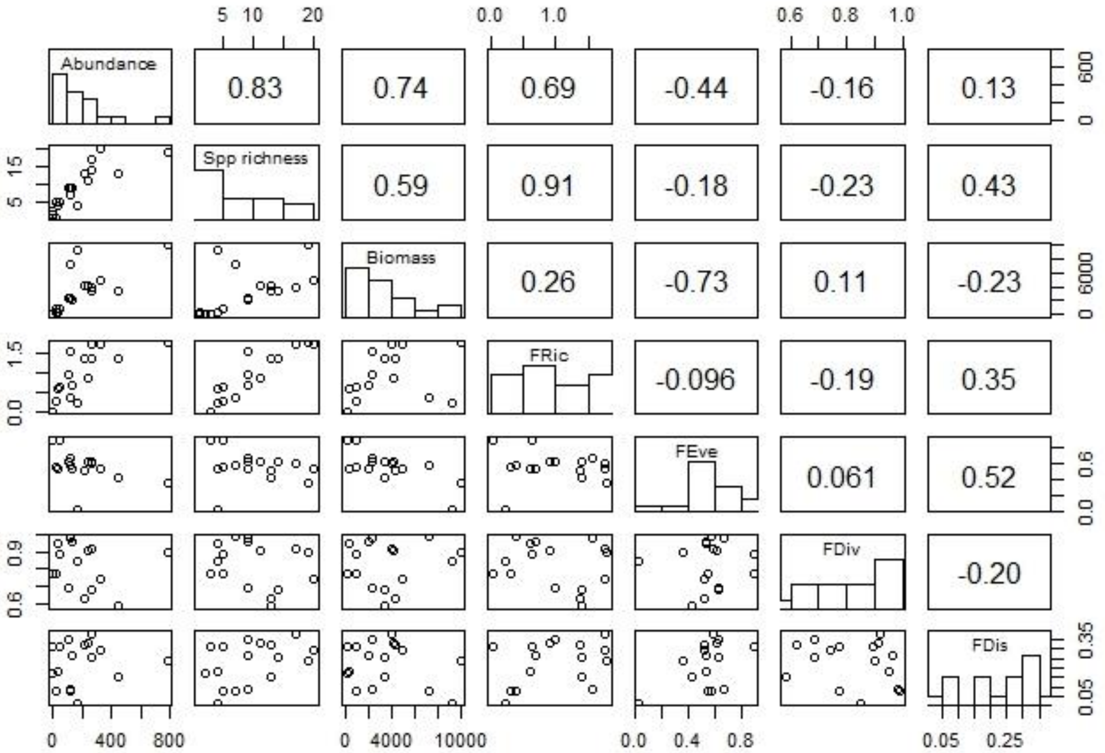


Figure S3.8 Associations between dung beetle community attributes: bivariate plots (lower panels), distributions (diagonal), and Pearson's ρ (upper panels).

Table S3.5 Pairwise comparisons of Bray Curtis assemblage similarity between different habitat categories. P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Asterisks indicate significant differences between categories at the 0.05 level. Degrees of freedom in all models = 1.

	P		**YR**		**MR**		**OR**	
	R^2	**Pr(>F)**	**R^2**	**Pr(>F)**	**R^2**	**Pr(>F)**	**R^2**	**Pr(>F)**
YR	0.14	0.472	-	-	-	-	-	-
MR	0.41	0.033*	0.23	0.076	-	-	-	-
OR	0.36	0.029*	0.18	0.266	0.05	0.824	-	-
RF	0.51	0.023*	0.26	0.025*	0.21	0.250	0.14	0.502

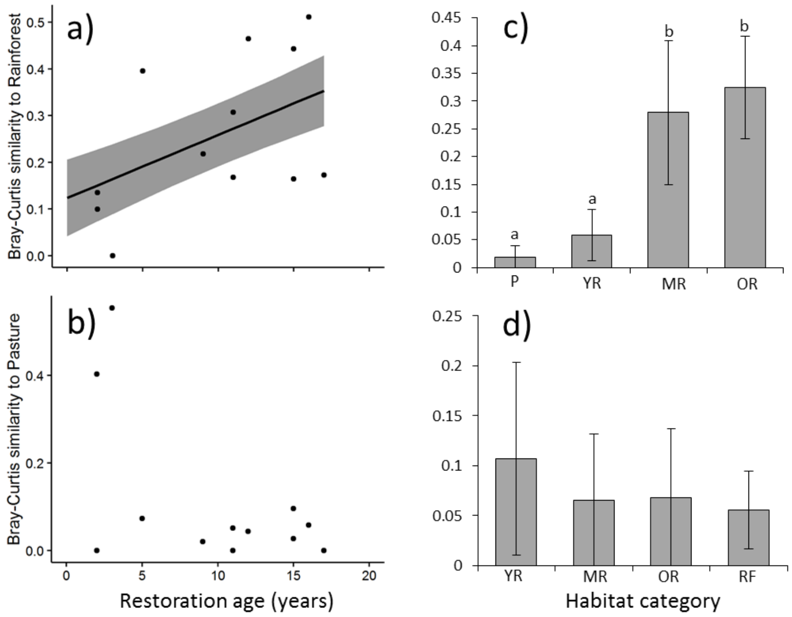


Figure S3.9 Relationship between restoration age and dung beetle assemblage similarity (Bray–Curtis index) to primary forest and pasture (a-b). Mean ± SE dung beetle assemblage similarity (Bray–Curtis index) to primary forest and pasture in the different habitat categories (c-d). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

Table S3.6 Support for generalized linear mixed models predicting multifunctionality, dung removal, seed dispersal and soil excavation in relation to dung beetle community attributes and functional diversity metrics.

Predictor	log(L)	ΔAIC_c	w_i
Multifunctionality			
FDiv	-17.04	0.00	0.309
FDis	-17.08	0.08	0.297
FEve	-17.37	0.66	0.223
Biomass	-18.02	1.95	0.116
FRic	-19.05	4.02	0.041
Abundance	-20.51	6.93	0.010
Species richness	-21.34	8.59	0.004
Dung removal			
FDis	-12.54	0.00	0.568
FEve	-13.83	2.57	0.157
FDiv	-13.86	2.65	0.151
Biomass	-14.78	4.49	0.060
FRic	-14.95	4.82	0.051
Abundance	-16.90	8.71	0.007
Species richness	-17.06	9.04	0.006
Seed dispersal			
FDis	-12.59	0.00	0.401
FDiv	-13.13	1.07	0.235
FEve	-13.41	1.64	0.176
Biomass	-13.85	2.52	0.114
FRic	-14.63	4.07	0.053
Abundance	-16.02	6.86	0.013
Species richness	-16.46	7.73	0.008
Soil excavation			
FDis	-16.23	0.00	0.432
FDiv	-16.56	0.66	0.310
FEve	-17.40	2.34	0.134
FRic	-17.84	3.21	0.087
Biomass	-18.83	5.19	0.032
Abundance	-20.97	9.49	0.004
Species richness	-21.68	10.90	0.002

* Abundance and Biomass were square root transformed to satisfy assumptions of normality. Block was included as a random effect in each model (n = 20 sites). There were 4 parameters in each model and 5 degrees of freedom. log(L) is the log likelihood; ΔAIC_c is the difference between the AIC_c of each model and that of the top model; and w_i is the Akaike weight.

Chapter 4

Investigating responses of leaf litter decomposition rates to tropical forest restoration and microhabitat conditions

4.1 SUMMARY

- Conversion of forest to agriculture is widespread and is known to cause substantial deterioration in soil properties. Rates of tropical forest recovery on previously cleared land are highly variable and natural regeneration of tropical forests may not occur at all if the system has attained a new stable state. Therefore, the restoration or reforestation of tropical forest on degraded land requires the restoration of suitable soil conditions. Litter fall and leaf decomposition are fundamental ecosystem processes in tropical forests, representing one of the major pathways of nutrient cycling, crucial for restoring soil condition.
- This study investigates how leaf litter decomposition rates and key biophysical parameters vary along a restoration chronosequence, and compares restored areas with reference (rainforest) and degraded (pasture) systems. The relationship between biophysical parameters and decomposition rates within a restoration setting was also investigated.
- Forest restoration leads to a marked increase in decomposition rates, accompanied by increased loss of mass, carbon and nitrogen from litterbags relative to pastures. The presence of soil invertebrate macrofauna significantly increased decomposition rates. Reforestation creates less hostile, more stable microclimatic conditions, which are cooler, moister and characterised by less variation in temperature and humidity than pastures. Reforestation also increases leaf and woody litter volume, creating a heterogeneous litter layer.
- Biophysical parameters accounted for a large amount (59-92%) of the variation in leaf litter decomposition rate. Overall, the most important factors influencing leaf litter decomposition rate were temperature variability (which has a negative effect on decomposition) and the amount of woody debris and leaf litter (both having a positive effect on decomposition).
- *Synthesis and Applications.* This study has shown that through the establishment of ecologically restored plantings, previously cleared land can recover stable microclimatic conditions and an established litter layer, which enhances decomposition rates and improves nutrient turnover. Furthermore, this study highlights the importance of recovering structural complexity in the litter layer to

enhance decomposition rates. Therefore, the addition of leaf litter and fine woody debris in restoration plantings, where possible, is advocated.

Key-words: leaf litter, woody debris, decomposition, nutrient cycling, turnover, soil condition, ecological restoration, ecosystem function, reforestation, tropical forest, wet tropics

4.2 INTRODUCTION

Tropical rainforests are globally important ecosystems due to their exceptionally high diversity and unique biota (Gaston 2000, Myers et al. 2000). Disturbance or degradation of tropical rainforests leads to deterioration in soil chemical, physical, and biological properties, which further limits the availability of essential soil nutrients (Rasiah et al. 2004, Parsons and Congdon 2008, Silveira et al. 2009). One of the major drivers of tropical forest degradation is clearing for agricultural practices (Achard et al. 2002), including cattle grazing. In Australia, nearly two-thirds of land has been modified for human use, with almost 90% of agricultural land being devoted to grazing (Bureau of Rural Sciences 2006). Conversion of forest to grazing pasture is known to cause substantial changes to a number of soil properties, most notably acidity, base exchange, porosity, nitrogen mineralisation, and nitrification (Reiners et al. 1994, Holt et al. 1996). In some tropical forest landscapes, areas that were initially cleared for pasture and cattle grazing are eventually abandoned, due to declining productivity of pasture grasses, ongoing soil degradation, invasion of unpalatable grasses and changing socio-economic incentives (Hobbs and Cramer 2007, Grau and Aide 2008).

Rates of tropical forest recovery on previously cleared land are highly variable (Holl 2007, Chazdon 2008b, Goosem et al. 2016) compared to other degraded ecosystems that can recover on timescales of decades to half centuries (Jones & Schmitz 2009). Land-use history interacts with biotic and abiotic factors to influence the rate and nature of recovery processes in tropical forests, and may not occur at all if the system has attained a new stable state (du Toit et al. 2004, Folke et al. 2004). The recovery pathway of forest that is converted to grazing pasture often leads to an alternative stable state because of the loss of soil organic matter and a reduction in soil fertility (Lamb et al. 2005). Ecological restoration of rainforest is therefore being increasingly applied worldwide and is an important strategy for reversing or mitigating biodiversity losses and enhancing ecosystem services in these recovering tropical forests (Brudvig 2011, Holl 2011, Holl and Aide 2011).

Litter fall and leaf decomposition are fundamental ecosystem processes in tropical forests, representing one of the major pathways of nutrient cycling (Vitousek 1984, Aber and Melillo 1991, Gill and Jackson 2000), crucial for restoring soil condition and maintaining plant and forest productivity (Defries et al. 2004, Moore et al. 2006, Li and Ye 2014). Litter decomposition is particularly important in the tropics because of the low nutrient storage capacity and the high turnover and uptake of nutrients in tropical soils. Epigaeic invertebrates contribute more to litter decomposition in the tropics, where the climate is favourable and stable, than at higher latitudes (González and Seastedt 2001, Wall et al. 2008, Yang and Chen 2009). Thus the restoration or reforestation of tropical forest on degraded land requires the restoration of suitable soil conditions.

Leaf litter decomposition is also a suitable process for assessing the ecological integrity of restored and recovering forests, due to its central role in ecosystem functioning. Leaf litter decomposition provides an indication of nutrient cycling and soil quality, as well as soil mesofauna activity and the performance of the decomposer subsystem. Soil faunal activity in itself can also be a good indicator of soil health and forest recovery, since many epigaeic invertebrates rely almost entirely upon the resources provided by the organic leaf litter layer (Holloway and Stork 1991; Stork and Eggleton 1992; Giller 1996) and so are unable to avoid the impact of local habitat change and thus have to respond to pressure effects *in situ*.

In this study, the recovery of leaf litter decomposition rates during tropical forest restoration is investigated in the Wet Tropics World Heritage region of north-eastern Australia. This study examines (1) whether leaf litter decomposition rates increase with time since restoration started; (2) how the successional stage of restoration affects key biophysical parameters associated with leaf litter decomposition (mean temperature and humidity, variability in temperature and humidity, mean woody and leaf litter volume, soil pH and soil bulk density); and (3) the relationships between biophysical parameters and decomposition rate.

4.3 MATERIALS AND METHODS

4.3.1 Study area

The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-elevation (500-1000 m) plateau in north-east Queensland, Australia (approximately 17°- 17°30’ S, 145°30’- 145°45’ E). The climate is predominantly humid tropical with temperatures of 15.6°C – 25.3°C (Bureau of Meteorology 2016) and rainforests are mostly complex notophyll to mesophyll vine-forest (Stanton and Stanton 2005). Most rainforests on the Tableland were cleared for agriculture 80 - 100 years ago, although small patches of remnant rainforest remain, and large (>3,000 ha) tracts of unfragmented rainforest survive on steeper hillsides. In recent decades there has been an expansion of rainforest restoration projects, with a high diversity (10 - 100+ species) of native rainforest trees and shrubs planted at high densities (ca. 3000 - 6000 stems/ha), in small (<5 ha) patches and strips, mainly in riparian areas (Goosem and Tucker 2013). The resulting landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant rainforest, natural regrowth and replanted forests.

4.3.2 Study design

Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years (n=1). These restoration sites were categorised into young (1-5 years), mid-age (6-12 years) and old (13-17 years) restoration categories. All restoration sites were previously grazed pasture. Remnant rainforest patches were considered as the reference target sites, representing the desired end point of restoration (n=4) and ungrazed, abandoned (for between 3 and 10 years) pasture on previously cleared rainforest land as the reference degraded sites (n=4), representing the starting point of restoration. Sample sites were set up in four blocks within the landscape (Figure S4.4), with each block containing one site of each of the three restoration categories and starting and reference sites: pasture; young restoration planting; mid-age restoration planting; old restoration planting; and rainforest. Blocks were selected to represent the maximum variation in topographic, climatic and geological parameters in the landscape so all sites within a block were similar in these parameters. Sites were separated by >300 m and blocks by >1.5 km. All restoration and degraded pasture sites were of similar size and shape (1 – 4 ha) and were 200 – 1000 m from intact rainforest, connected through restored and remnant corridors. All rainforest reference sites were at least 300 ha in size. A 50m x 20m study plot was established in the centre of each site, within which all sampling took place. Two sub-plots were established at each study plot, at 5m and 45m along the centre line, within which litterbags were installed.

4.3.3 Leaf litter decomposition

To examine *in situ* leaf-litter decomposition, the litterbag method was used (Bocock and Gilbert 1957, Singh and Gupta 1977, Harmon et al. 1999). Litterbags (see below) were filled with leaves from a selection of six common tree species at the rainforest sites and that were used in restoration replantings in the study area: *Acronychia acidula, Alphitonia petriei, Cardwellia sublimis, Elaeocarpus angustifolius, Neolitsea dealbata* and *Flindersia brayleyana*. Mature leaves were cut from rainforest trees during the dry season in 2013, the petioles were removed and the leaves were oven-dried at 35°C until a constant weight was reached. Each litterbag was filled with 5 g of dried, mixed leaves from the six tree species. Five grams was chosen as this is consistent with other studies in the area and was sufficient to ensure adequate litter mass remaining after the decomposition period (e.g. Parsons and Congdon 2008, Parsons et al. 2011, Parsons et al. 2012). Litterbags (20 cm x 25 cm) were constructed from fibreglass fly-screen material of mesh size 1.5 mm x 1.5 mm, and sealed using a plastic heat sealer. The mesh size of 1.5 mm was sufficiently small to allow mesofauna (100 µm - 2 mm) but not macrofauna (>2 mm) to enter, and prevented the loss of litter due to breakage (Crossley and Hoglund 1962, Swift et al. 1979, Bradford et al. 2002, St. John et al. 2011).

The rate at which litter decomposes is influenced by the composition of soil organisms (macrofauna) (González and Seastedt 2001, Bradford et al. 2002, Vasconcelos and Laurance 2005, Ayres et al. 2009, Powers et al. 2009b). The effect of soil macrofauna activity on litter decomposition was investigated by constructing a subset of litterbags that allowed access by macrofauna (IF). These litterbags were constructed as outlined above but had eight 1 cm^2 perforations on both sides of the bags to allow macrofauna access (Vasconcelos and Laurance 2005, Barlow et al. 2007). The bags excluding macrofauna (EF) had no perforations. Litterbags were laid out on the forest floor in arrays, with eight litterbags (four EF bags and four IF bags), each 5cm apart, placed at each subplot. Litterbags were placed on the soil surface with a thin layer of litter over the top (where available) and secured in place with a metal peg. Litterbags were installed in October 2013 during the end of the dry season, and half were collected during the wet season in January 2014 (after 3 months) and half collected after the wet season in April 2014 (after 6 months). During each collection, four litterbags were removed from each plot (two IF litterbags; two of EF litterbags) at each site (totalling eight litterbags per site).

Actual rates of decomposition may be overestimated by using non-senescent green leaves (Woods and Raison 1982). Naturally senesced leaves could not be used for the entirety of the study because of limited availability. An additional subset of litterbags (n = 128) using naturally senesced, fallen leaves of the same six tree species, were placed in pastures and at rainforest sites to assess their relative rates of decomposition and to determine whether differences in decomposition rates between cut and fallen leaves were constant between different habitats. Litterbags containing fallen leaves were prepared in the same way as those containing cut leaves and were installed in pasture and rainforest sites only. A subset of twenty control litterbags (cut and fallen leaves) were kept aside from those deployed in the field to determine initial chemical characteristics of the leaves. An additional set of twenty litterbags were used as 'travel bags' and were weighed, transported to and from the field sites and then re-weighed. The average proportion of mass lost from transport was deducted from the initial mass of each litterbag deployed in the field, to correct for leaf loss during travel to and from the field sites.

4.3.4 Chemical analysis

Following removal from the field, fine root matter, grass, termite runs and mud were removed from the outside of the litterbags and the litterbags were gently rinsed under running water to remove any soil. All control litterbags (kept in the lab) and litterbags removed from the field were then oven-dried at 65°C until a constant weight was reached and then weighed to compare pre-and post-decomposition mass. Litterbag contents were milled, and analysed for %C and %N on an Elementar Vario EL elemental analyser (Hanau, Germany), and for total P concentration using the Kjeldahl digestion method with an autoanalyser (Anderson and Ingram 1989). The initial chemical characteristics of the leaves were determined from the control samples (both cut and fallen).

4.3.5 Biophysical parameters

Eight biophysical parameters associated with litter decomposition were examined at each study site. Temperature and humidity were recorded during the study period (October 2013 – April 2014) using Hygrochron iButton® data-loggers, with one logger at the centre of each study plot, beneath the leaf litter layer, which recorded hourly temperature and humidity to 0.1°C. The mean and coefficient of variation (as a measure of variability) were calculated from the temperature and humidity data collected and used for the analysis.

Woody litter and leaf litter volume were measured within three 50cm x 50cm quadrats placed at 5m, 25m and 45m along the centre line of the study plot. All woody and leaf litter from within the quadrat was collected and all topsoil removed, before the litter was oven-dried at 60°C until a constant weight was achieved. Mean woody and leaf litter volume was calculated for each site as the average of dry mass of woody and leaf litter for the 3 quadrats. Two soil cores (30 mm diameter x 10 cm depth) were collected in April 2014 at 5m and 45m along the centre line of the study plot. All stones and roots were removed and the soil samples were dried at 60°C until a constant weight was achieved, then weighed and analysed for pH. Soil dry mass was used to calculate mean soil bulk density for each site.

4.3.6 Data analysis

Statistical analyses were carried out using R version 3.1.1 (R Core Team 2014). Data from the two sub-plots at each site were pooled. Four decomposition metrics were used to assess leaf litter decomposition (proportion of mass; carbon; nitrogen; and phosphorus lost). To test for the effects of restoration age and habitat category on decomposition (proportion of mass; carbon; nitrogen; and phosphorus lost) and biophysical parameters (mean temperature, mean humidity; variability in temperature ; variability in humidity ; woody litter volume; leaf litter volume; soil pH; and soil bulk density), generalised linear mixed effects models (glmm) were used with block as a random effect. The statistical significance of the predictor variable in each glmm was tested with analysis of variance (ANOVA). A contrast analysis was performed on the glmms with habitat category as a predictor, by obtaining confidence intervals using parametric bootstrapping to determine whether the response variables differed among the habitat categories. Appropriate error structures were applied for all models (Table S4.3).

An information-theoretic approach was used to evaluate the relationships between biophysical parameters and the decomposition metrics. All predictor variables were z-transformed (to a mean of 0 and standard deviation of 1) prior to modelling to make intercepts meaningful and allow comparisons between model coefficients (Schielzeth 2010). One outlier was identified using Cleveland dotplots and Cook's Distance and removed from the analysis. Glmms with Gaussian structures were fitted to each of the relevant community attributes as well as null models. The Akaike's Information Criterion corrected for small sample size (AIC_c) was used to evaluate models, by comparing the differences in AIC_c for each model with respect to the AIC_c of the best candidate model (Burnham and Anderson 2002). Based on the relative likelihoods of the different models, Akaike weights (w_i) were calculated to determine the weight of evidence in favour of each model being the best model in the set of candidate models, using the *MuMIn* package in R (Burnham and Anderson 2002). ANOVAs and contrast analyses were run on each glmm.

4.4 RESULTS

4.4.1 Effect of restoration on leaf litter decomposition

The proportion of mass lost (χ^2 =5.57, P = 0.018; Figure 4.1a) and carbon lost (χ^2 =4.04, P = 0.045; Figure 4.1b) from litterbags increased significantly with restoration age. The proportion of nitrogen (χ^2 =2.87, P = 0.09; Figure 4.1c) and phosphorus (χ^2 = 0.32, P = 0.572; Figure 4.1d) lost did not vary significantly with restoration age. The proportion of mass lost from litterbags differed among habitat categories (χ^2 = 37.23, df= 4, P <0.001; Figure 4.1e), and was lowest in pasture and young restoration and highest in mid-age and old restoration and rainforest. The proportion of carbon (χ^2 = 13.07, df = 4, P = 0.011; Figure 4.1f) and nitrogen lost (χ^2 = 13.51, df = 4, P = 0.009; Figure 4.1g) from litterbags differed among habitat categories being lowest in pasture, intermediate in young restoration, and highest in mid-age and old restoration and rainforest. The proportion of phosphorus lost from litterbags did not vary by habitat category (χ^2 = 5.92, df= 4, P = 0.205; Figure 4.1h).

Decomposition (measured as mass lost from litterbags) significantly varied by leaf type, with cut leaves experiencing higher levels of mass loss than fallen leaves (χ^2 = 9.40, df = 1, P = 0.002; Figure 4.2; Table S4.4). However, the difference in mass lost between cut or fallen leaves was consistent, regardless of habitat category (χ^2 = 0.13, df = 1, P = 0.717) or collection timing (χ^2 = 0.02, df = 1, P = 0.881). The presence of macrofauna increased decomposition rates (χ^2 = 13.87, df = 1, P < 0.001; Figure 4.2; Table S4.4) but this effect did not vary with restoration age (χ^2 = 2.50, df = 1, P = 0.114; Figure S4.6). Collection timing mattered (χ^2 = 47.62, df = 1, P <0.001; Figure 4.2), in that decomposition was faster in the first 3 months (51.2% ± 0.076 loss in mass over 3 months) than in the second 3 months (24.5% ± 0.014 loss in mass over

3 months; Table S4.4), but this effect did not vary with restoration age ($\chi^2 = 1.20$, df = 1, $P = 0.273$).

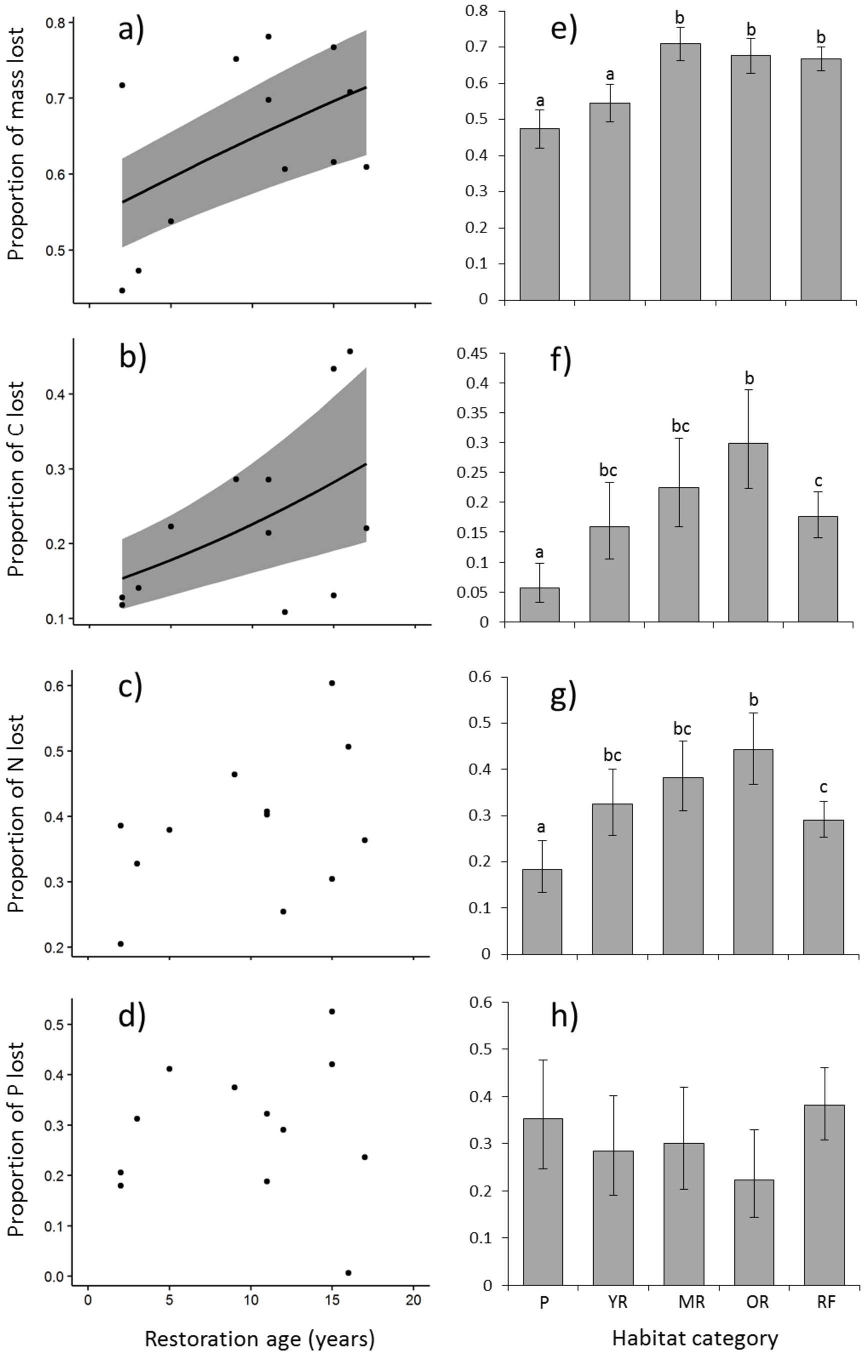


Figure 4.1 Relationship between restoration age and proportion of mass, carbon (C), nitrogen (N) and phosphorous (P) lost from litterbags (a-d). Mean ± SE proportion of mass, carbon (C), nitrogen (N) and phosphorous (P) lost from litterbags in the different habitat categories (e-h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

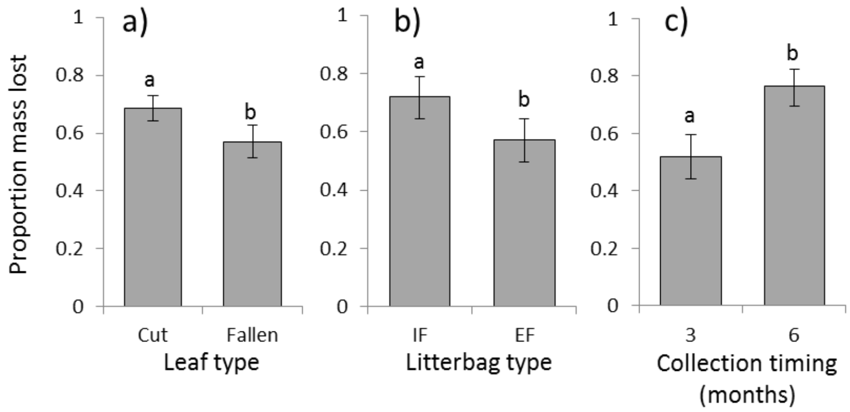


Figure 4.2 Mean ± SE proportion of mass lost from litterbags containing cut and fallen leaves (a); from litterbags including (IF) and excluding macrofauna (EF) (b); and from litterbags collected after three or six months (c). Unlike letters indicates significant differences at the ≤ 0.05 level.

4.4.2 Effect of restoration on biophysical parameters

Temperature variability (χ^2 = 14.20, *P* <0.001; Figure S4.7), humidity variability (χ^2 = 13.24, *P* <0.001; Figure S4.7) and mean temperature (χ^2 = 12.86, *P* <0.001; Figure S4.7) all decreased with restoration age; whereas mean humidity (χ^2 = 5.52, *P* = 0.019; Figure S4.7), woody litter volume (χ^2 = 18.02, *P* <0.001; Figure S4.7) and leaf litter volume (χ^2 = 4.14, *P* = 0.042; Figure S4.7) increased significantly with restoration age. Soil bulk density (χ^2 = 0.07, *P* = 0.792; Figure S4.7) and soil pH (χ^2 = 2.51, *P* = 0.113; Figure S4.7) were largely independent of restoration age, although bulk density was significantly lower in pasture and rainforest sites than in the restoration sites (Table 4.1). All biophysical parameters, except for mean humidity, were significantly different across habitat categories (Table 4.1). Generally, older restoration sites experienced less temperature and humidity fluctuation; were cooler; had more leaf and woody litter; lower soil pH; and bulk density than pasture sites. Older restoration sites were statistically indistinguishable from rainforest in temperature and humidity variability, mean temperature and leaf litter volume (Table 4.1).

Table 4.1 Mean ± SE biophysical parameters for each habitat category (from GLMM outputs): TempVar = temperature variability; HumVar = humidity variability; Temp = mean temperature; Hum = mean humidity; Wood = woody litter volume (g m^{-2}); Leaf = leaf litter volume (g m^{-2}); pH= soil pH; Bulk = soil bulk density (g cm^{-3}). Superscripts represent pairwise differences at the $P \leq 0.05$ level.

Biophysical parameter	**Pasture**	**Young restoration**	**Mid-age restoration**	**Old restoration**	**Rainforest**	χ^2	***P***
TempVar†	0.24 ± 0.02^{a}	0.18 ± 0.02^{b}	0.11 ± 0.02^{c}	0.09 ± 0.02^{c}	0.08 ± 0.02^{c}	52.70	<0.001
HumVar†	0.15 ± 0.03^{a}	0.16 ± 0.03^{a}	0.05 ± 0.02^{b}	0.04 ± 0.02^{b}	0.06 ± 0.02^{b}	9.77	0.045
Temp	22.78 ± 0.42^{a}	22.15 ± 0.42^{a}	20.70 ± 0.42^{b}	20.57 ± 0.45^{b}	20.16 ± 0.45^{b}	59.24	<0.001
Hum	92.53 ± 2.21	93.02 ± 2.22	92.39 ± 2.21	96.61 ± 2.66	94.91 ± 2.61	2.39	0.665
Wood	0.02 ± 0.29^{a}	0.22 ± 0.29^{a}	1.82 ± 0.34^{b}	2.48 ± 0.30^{b}	1.54 ± 0.30^{ab}	55.65	<0.001
Leaf	0.02 ± 0.01^{a}	0.31 ± 0.13^{b}	1.31 ± 0.56^{c}	1.48 ± 0.64^{c}	1.68 ± 0.72^{c}	81.44	<0.001
pH	5.65 ± 0.10^{a}	5.33 ± 0.10^{b}	5.10 ± 0.10^{bc}	5.20 ± 0.10^{b}	4.83 ± 0.10^{c}	39.24	<0.001
Bulk	0.78 ± 0.06^{a}	0.94 ± 0.06^{b}	0.91 ± 0.06^{b}	0.97 ± 0.06^{b}	0.65 ± 0.06^{a}	26.25	<0.001

†Coefficient of variance

4.4.3 Effect of biophysical parameters on decomposition

The biophysical parameters across the plots were uncorrelated, except for mean temperature, temperature variability, leaf litter volume and soil pH (Figure S4.8) The global model containing all biophysical parameters and the random effect (‘block’) accounted for 92.2% of the variation in mass lost from the litterbags ($R^2 = 0.922$; Table 4.2), 71.7% of the variation in nitrogen lost ($R^2 = 0.717$; Table S4.5), 70.0% of the variation in carbon lost ($R^2 = 0.700$; Table S4.5) and 58.7% of the variation in phosphorus lost ($R^2 = 0.587$; Table S4.5).

Table 4.2 Support for generalized linear mixed models predicting proportion of mass lost from litterbags in relation to biophysical parameters. The global model is shown in parentheses.

Predictor	**log(L)**	**AIC**	**ΔAIC$_c$**	w_i	***P***
(Mass ~ bulk + pH + temp + hum + temp.var + hum.var + litter + wood + (1|Block))					
Temperature variability	15.86	-20.643	0.00	0.46	<0.001
Woody litter volume	15.37	-19.661	0.98	0.28	<0.001
Leaf litter volume	14.90	-18.730	1.91	0.18	<0.001
Mean temperature	13.99	-16.907	3.74	0.07	<0.001
Humidity variability	10.88	-10.693	9.95	0.00	0.004
Soil pH	10.04	-8.994	11.65	0.00	0.017
Soil bulk density	8.59	-6.095	14.55	0.00	0.208
Mean humidity	7.91	-4.741	15.90	0.00	0.974

* Predictor variables were standardised using z-transformation and Block was included as a random effect in each model (n = 20 sites). There were 3 parameters in each model and 4 degrees of freedom. log(L) is the log likelihood; AICc is the Akaike’s information criterion corrected for small sample size; ΔAICc is the difference in AICc compared to the best ranked model; w_i is the Akaike weight; and P-values designate the effect of each parameter on the proportion of mass lost from litterbags. Mass = mass lost from litterbags; bulk -= soil bulk density; pH = soil pH; temp = mean temperature; hum = mean humidity; temp.var = temperature variability; hum.var = humidity variability; litter = leaf litter volume; wood = woody litter volume.

Of the eight biophysical parameters, temperature variability was the best predictor of decomposition, having a significant negative effect on mass lost (χ^2 = 27.63; *P* <0.001; Table 4.2; Figure 4.3), nitrogen lost (χ^2 = 7.58; *P* = 0.006; Table S4.5) and carbon lost (χ^2 = 8.84; *P* = 0.003; Table S4.5) from litterbags. Woody litter volume was the second best predictor of decomposition, with mass lost (χ^2 = 28.54, *P* <0.001; Table 4.2; Figure 4.3), nitrogen lost (χ^2 = 6.91, *P* = 0.009; Table S4.5) and carbon lost (χ^2 = 4.63, *P* = 0.031; Table S4.5) all increasing with woody litter volume. Leaf litter volume was also a good predictor of decomposition, having a significant positive effect on mass lost (χ^2 = 23.24, *P* = 0.010; Table 4.2; Figure 4.3) and nitrogen lost (χ^2 = 4.23, *P* = 0.039; Table S4.5) from litterbags. The best predictors of phosphorus lost from the litterbags were soil bulk density (χ^2 = 2.96, *P* = 0.086; Table S4.5), soil pH (χ^2 = 1.68, *P* = 0.195; Table S4.5), temperature variability (χ^2 = 0.65, *P* = 0.420; Table S4.5) and humidity variability (χ^2 = 0.51, *P* = 0.474; Table S4.5). However, there was very little difference in the strength of evidence between the different phosphorus models, and none of the biophysical parameters had a significant effect on phosphorus lost from litterbags.

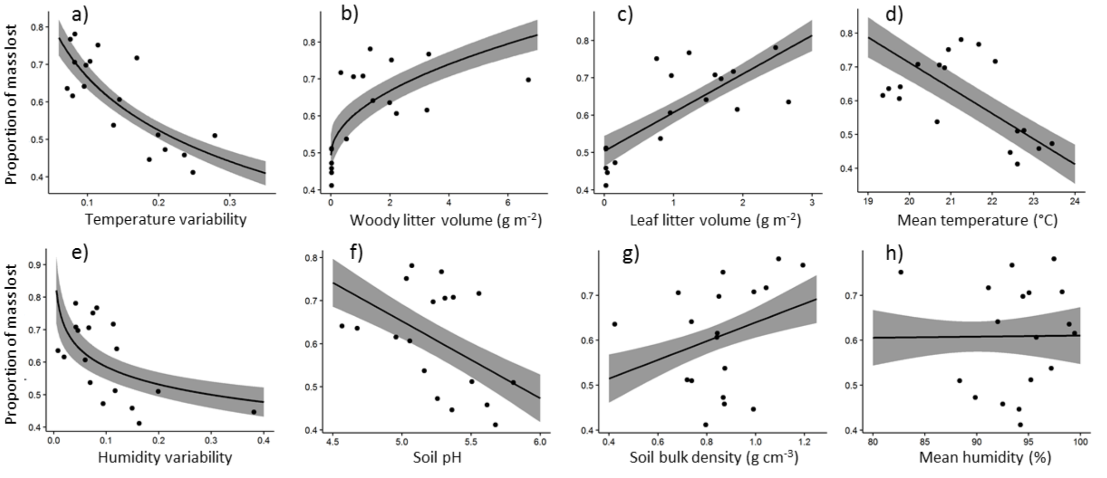


Figure 4.3 The effect of eight biophysical parameters on the proportion of mass lost from litterbags. Models were generalised linear mixed effect models with Gaussian error distributions. Temperature and humidity variability measured as coefficient of variation.

4.5 DISCUSSION

The patterns reported here demonstrate that reforestation does aid the recovery of leaf litter decomposition in a relatively short time (10-17 years). Ecological restoration of previously forested pasture increased the overall litter decomposition rate and nutrient release from leaf litter back into the soil. Reforestation creates less hostile, more stable microclimatic conditions, which are cooler, moister and characterised by less variation in temperature and humidity than pastures. Reforestation also increases leaf and woody litter volume, which creates a heterogeneous litter layer and microhabitat that promotes the decomposition process and maintains epigaeic meso- and macrofauna. The most important biophysical drivers of leaf litter decomposition were low temperature variability, and high leaf and woody litter volume.

4.5.1 Effect of restoration, macrofauna, leaf type and seasonality on leaf litter decomposition

Forest restoration leads to a marked increase in decomposition rates, demonstrated by increased loss of mass, carbon and nitrogen from litterbags relative to pastures. This finding accords with previous studies where decomposition rates decreased with increased forest disturbance (Ewel 1976, Kumar and Deepu 1992, Barlow et al. 2007, Parsons and Congdon 2008, Silveira et al. 2009). It has been suggested that trees could promote soil communities that are particularly capable of degrading the litter they encounter most often. The ‘home-field advantage’ (HFA) hypothesis predicts that plant litter will decompose faster when placed in habitat which it was derived (‘home’) than in a foreign habitat (‘away’), resulting in different soil communities associated with different plant species (Ayres et al. 2009). The increased decomposition rates in older restoration sites may therefore indicate specialisation of soil biota in the decomposition of litter produced by forest tree species.

Litter in litterbags including macrofauna decomposed faster than in litterbags excluding macrofauna, highlighting the importance of larger invertebrates in litter decomposition processes. Soil macrofauna such as earthworms, termites, and millipedes disaggregate litter increasing the surface area of leaves and twigs for smaller invertebrates to decay, thereby promoting decomposition (Coleman et al.

2004, Bardgett 2005). As such, the establishment of suitable microclimates and habitats for macrofauna is an important element of forest restoration management in order to recover decomposition processes. Furthermore, the lack of a significant interaction between litterbags with and without macrofauna and habitat category suggests that there may be very little species turnover across the restoration gradient; or that there is a high level of functional redundancy in the macrofauna community, in that the community has the same effect on leaf litter decomposition rates, regardless of species composition. In terms of methodology, the lack of a significant interaction between between litterbags including and excluding macrofauna, and habitat category suggest that the effects of litterbag type (IF/ EF) were consistent over the time of the study. It is therefore suggested that litterbags both including and excluding macrofauna should be used in conjunction for assessing leaf litter decomposition rates.

Cut leaves displayed higher decomposition rates than fallen leaves, likely caused by their higher nutrient content, as nutrient-rich leaves are more rapidly consumed by invertebrates and experience greater microbial activity (Woods and Raison 1982). Although the use of cut leaves likely overestimates absolute natural decomposition rates, the difference in mass lost between cut and fallen leaves did not vary among site age classes, and cut leaves are a suitable substitute for naturally abscised leaves when comparing relative rates of decomposition. Decomposition rates varied according to season, in that decomposition was faster during the wetter first three months than during the drier second three months; however, this effect was consistent across site ages. Since litter decomposition can be influenced by different factors at different stages of decomposition (Loranger et al. 2002), it is recommended that future studies take into account seasonality and timing when looking at comparative decomposition rates.

4.5.2 Effect of restoration on biophysical parameters

Restoration sites were cooler, more humid, with less variation in temperature and humidity, and more leaf litter and woody debris, consistent with other studies (Chen et al. 1999, Jennings et al. 1999, Kanowski et al. 2003). Reference pasture sites on the other hand, were hotter, drier, suffered more extremes in temperature and humidity and had very little leaf litter and woody debris. A shift in environmental conditions occurred between young and mid-age restoration sites, corresponding with the average time in which high canopy closure (>70%) occurs (3 - 5 years) (Kanowski et al. 2003, Nakamura et al. 2003, Grimbacher and Catterall 2007, Hobbs 2012, Goosem and Tucker 2013). Indeed, the forest canopy is one of the chief determinants of the microhabitat within a forest, and the closure of the canopy and establishment of large saplings is a crucial requirement for effective restoration plantings.

Litter cover is important too in restoration planting as it slows soil desiccation and buffers the soil surface against fluctuations in temperature and water content (MacKinney 1929, Walsh and Voigt 1977, Ginter et al. 1979, Benkobi et al. 1993, Ogée and Brunet 2002, Sayer 2006), providing a cooler, moister, more stable microclimate which may enhance mineralisation rates, and therefore nutrient availability (e.g. Knapp and Seastedt 1986). The microclimate maintained by the litter layer may be favourable to herbivores and pathogens and so is also important in determining later seedling survival and performance (Sayer 2006).

The creation of reforested habitats containing increased litter has important implications for ecosystem functions, as well as for biodiversity, including reptiles (Kanowski et al. 2006, Shoo et al. 2014), amphibians (Shoo et al. 2011) and beetles (Grove 2002, Nakamura et al. 2003, Grimbacher et al. 2006), which all demonstrate a preference for cooler, moist habitats with an established litter layer and woody debris in tropical forests. In fact, globally, environments supporting diverse species generally have mild, warm conditions with little seasonal variation, that can be tolerated by many species (Giller 1996).

4.5.3 Effect of biophysical parameters on decomposition rate

Biophysical parameters accounted for a large amount (59-92%) of the variation in leaf litter decomposition rate. Overall, the most important factors influencing leaf litter decomposition rate were temperature variability and the amount of woody debris and leaf litter cover, followed by mean temperature and humidity variability. This finding is in accordance with a study by Barlow et al. (2007) who demonstrated that leaf fall (and therefore leaf litter availability) is the factor most consistently correlated with leaf litter decomposition in a tropical system.

A consistently moist, heterogeneous litter layer provides insulation against temperature and moisture extremes and leads to greater microbial biomass and activity in decomposing litters (Donnelly et al. 1990). These conditions also provide habitats and resources for the decomposer community, including earthworms (Arpin et al. 1995, Gonzalez and Zou 1999), arthropods (Nakamura et al. 2003), oribatid mites (Hansen 2000), fungi (Tyler 1991), and soil micro-organisms (Giller 1996, Jordan et al. 2003).

4.5.4 Management and conservation implications

The main pathway for nutrient cycling in terrestrial systems is litter decomposition (Vitousek 1984, Aber and Melillo 1991, Coleman and Crossley 1996, Sayer 2006). Effective litter decomposition is therefore crucial in forest recovery as it mineralises nutrients, making them available to plants, and also improves soil quality (MacLean and Wein 1978, Moore et al. 2006). The growth of tree seedlings, especially in their early stages, and total plant biomass production, is strongly affected by the availability of soil nutrients, particularly nitrogen turnover and phosphorus (Vitousek 1984, Tilman 1986, Nussbaum et al. 1995, Burslem 1996, Hättenschwiler and Vitousek 2000, Paul et al. 2010). An increase in the input of nutrients from decomposing leaf litter in restored sites thus aids forest successional recovery in restored forests.

Litter decomposition is particularly important in the tropics because of the low nutrient storage capacity and the high turnover and uptake of nutrients in tropical soils. Furthermore, the disturbance and degradation experienced by previously forested areas in north Queensland has resulted in depauperate soils with limited nutrient availability. Poor soil quality provides a further barrier to successional recovery, one that needs to be addressed in ecological restoration projects. Habitat features such as fine and coarse woody debris and an established leaf litter layer can be slow to develop on formerly degraded land and can consequently pose persistent barriers to the re-establishment of vegetation and specialist species (Catterall et al. 2008). This study recommends the addition of leaf litter and woody debris in young restoration plantings to contribute to the structural complexity and to enhance decomposition rates. The addition of litter in plantings may help offset a more open canopy, by providing better insulation against temperature and moisture extremes, as well as more resources for colonising soil and litter arthropods (Majer et al. 1984, Greenslade and Majer 1993, Nakamura et al. 2003). Some restoration practitioners now include coarse woody debris manipulation in large-scale restoration projects (e.g. Shoo et al. 2011, Manning et al. 2013, Shoo et al. 2014), but this study also advocates the addition of fine woody debris where possible.

4.5.5 Conclusions

This study demonstrates that through the establishment of ecologically restored plantings, previously cleared land can recover stable microclimate conditions, and an established litter layer, which enhance decomposition rates and improve nutrient turnover. These findings highlight the importance of encouraging fast recovery of plantings, including establishing early canopy closure (e.g. through grass and weed control and high density plantings) to initiate a positive feedback loop in which early canopy closure decreases temperature variation in the litter layer and improves decomposition rates and nutrient turnover, providing more suitable conditions for the establishment and survival of forest tree species. Faster establishment and recovery of plantings will assist in stemming the tide of species and habitat loss, as well as increasing carbon storage.

4.6 SUPPORTING INFORMATION

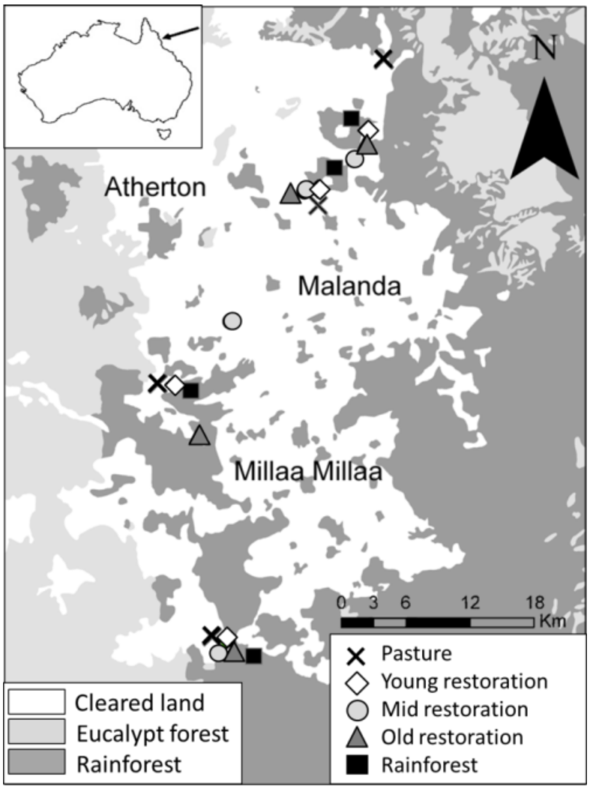


Figure S4.4 Map of the study area, showing the 20 study sites and areas of cleared forest, Eucalypt forest and rainforest.

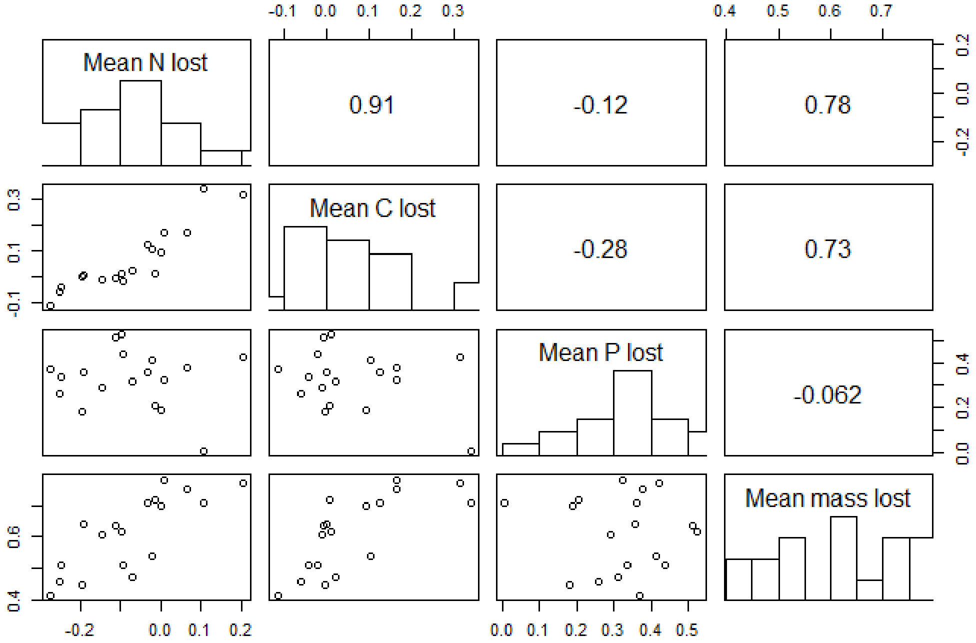


Figure S4.5 Associations between litter decomposition metrics: bivariate plots (lower panels), distributions (diagonal), and Pearson's ρ (upper panels).

Table S4.3 Structure of generalised linear mixed models for determining the effects of restoration age and habitat category on leaf litter decomposition and biophysical parameters.

	Fixed effect: Restoration age		Fixed effect: Habitat category	
Response variable	**Error distribution**	**Transformation**	**Error distribution**	**Transformation**
Decomposition metric				
Mass lost	Beta		Beta	
Phosphorus lost	Beta		Beta	
Carbon lost	Beta		Beta	
Nitrogen lost	Beta		Beta	
Multifunctionality	Gaussian		Gaussian	
Biophysical parameter				
Mean temperature	Gaussian		Gaussian	
Mean humidity	Gaussian	log(10)	Gaussian	log(10)
Temperature variance	Binomial (logit)		Binomial (logit)	
Humidity variance	Beta		Beta	
Woody litter volume	Gaussian		Gaussian	log(10)
Leaf litter volume	Gaussian		Gaussian	log(10)
Soil pH	Gaussian		Gaussian	
Soil bulk density	Gaussian	log(10)	Gaussian	log(10)

Table S4.4 Mean ± SE proportion of mass lost from litterbags containing cut and fallen leaves; from litterbags including (IF) and excluding macrofauna (EF); and from litterbags collected after three months and six months (c). Superscripts indicate significant differences at the ≤ 0.05 level.

Litterbag variable	Proportion of mass lost ± SE
Leaf type	
Cut	0.687 ± 0.687^{a}
Fallen	0.571 ± 0.229^{b}
Litterbag type	
IF	0.722 ± 0.072^{a}
EF	0.572 ± 0.076^{b}
Collection timing	
3 months	0.519 ± 0.076^{a}
6 months	0.765 ± 0.062^{b}

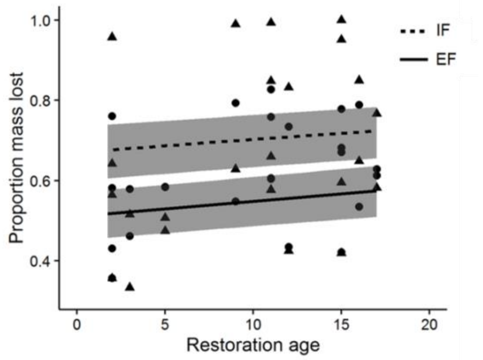


Figure S4.6 Relationship between restoration age and proportion of mass lost from litterbags including (IF) and excluding (EF) macrofauna. Triangles represent litterbags including macrofauna (IF) and circles represent litterbags excluding macrofauna (EF).

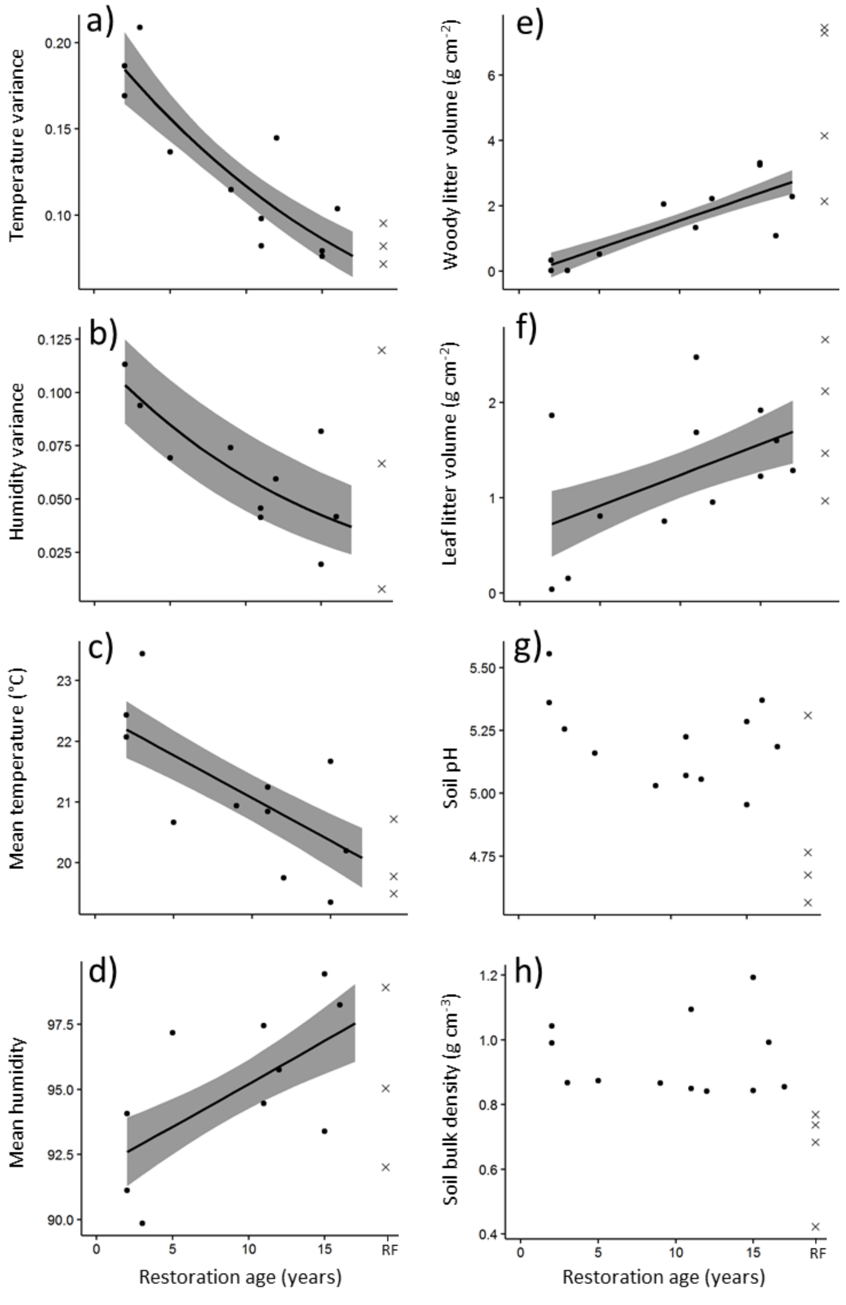


Figure S4.7 Relationship between restoration age and biophysical parameters (a-h), including mean rainforest reference values (RF).

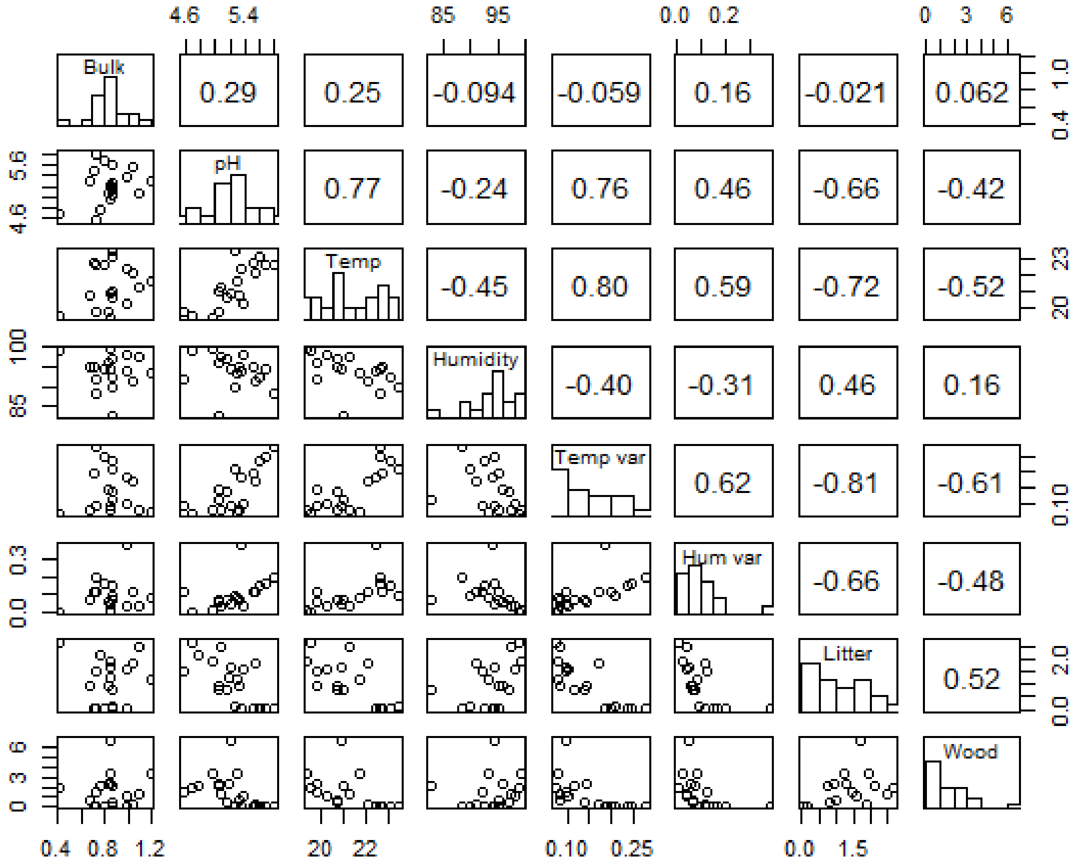


Figure S4.8 Associations between biophysical parameters: bivariate plots (lower panels), distributions (diagonal), and Pearson's ρ (upper panels).

Table S4.5 Support for generalized linear mixed models predicting proportion of nitrogen, carbon and phosphorus lost from litterbags in relation to biophysical parameters. Global models are shown in parentheses.

Predictor	**log(L)**	**AIC**	**ΔAIC_c**	**w_i**	**P**
Nitrogen lost					
(N lost ~ bulk + pH + temp + hum + temp.var + hum.var + litter + wood + (1|Block))					
Temperature variance	9.64	-8.204	0.00	0.35	0.006
Woody litter volume	9.37	-7.656	0.55	0.27	0.009
Soil bulk density	8.93	-6.776	1.43	0.17	0.018
Leaf litter volume	8.41	-5.750	2.45	0.10	0.040
Humidity variance	7.46	-3.847	4.36	0.04	0.162
Mean temperature	7.15	-3.232	4.97	0.03	0.248
Soil pH	6.68	-2.277	5.93	0.02	0.597
Mean humidity	6.59	-2.094	6.11	0.02	0.758
Carbon lost					
(C lost ~ bulk + pH + temp + hum + temp.var + hum.var + litter + wood + (1|Block))					
Temperature variance	11.04	-11.006	0.00	0.52	0.003
Soil bulk density	10.12	-9.161	1.84	0.21	0.013
Woody litter volume	9.54	-7.996	3.01	0.12	0.031
Leaf litter volume	8.77	-6.472	4.53	0.05	0.099
Mean temperature	8.34	-5.607	5.40	0.04	0.127
Humidity variance	8.13	-5.179	5.83	0.03	0.242
Soil pH	7.71	-4.351	6.66	0.02	0.532
Mean humidity	7.56	-4.041	6.97	0.02	0.784
Phosphorus lost					
(P lost ~ bulk + pH + temp + hum + temp.var + hum.var + litter + wood + (1|Block))					
Soil bulk density	9.61	-8.142	0.00	0.30	0.086
Soil pH	9.01	-6.943	1.20	0.17	0.195
Temperature variance	8.54	-6.011	2.13	0.10	0.42
Humidity variance	8.48	-5.892	2.25	0.10	0.474
Mean humidity	8.41	-5.751	2.39	0.09	0.678
Mean temperature	8.39	-5.700	2.44	0.09	0.678
Woody litter volume	8.28	-5.479	2.66	0.08	0.704
Leaf litter volume	8.24	-5.412	2.73	0.08	0.953

* Predictor variables were standardised using z-transformation and Block was included as a random effect in each model (n = 20 sites). There were 3 parameters in each model and 4 degrees of freedom. log(L) is the log likelihood; AICc is the Akaike's information criterion corrected for small sample size; ΔAICc is the difference in AICc compared to the best ranked model; w_i is the Akaike weight; and P-values designate the effect of each parameter on the decomposition metric. bulk -= soil bulk density; pH = soil pH; temp = mean temperature; hum = mean humidity; temp.var = temperature variability; hum.var = humidity variability; litter = leaf litter volume; wood = woody litter volume.

Chapter 5

Determining the biophysical drivers of biodiversity and ecosystem functioning recovery through ecological restoration

5.1 SUMMARY

- Ecological restoration aims to initiate or accelerate the recovery of an ecosystem with respect to its health, integrity and sustainability. The success of restoration activities depends on a myriad of ultimate (indirect) and proximate (direct) variables operating simultaneously across multiple spatial scales, predominantly restoration age, disturbance history and landscape context.
- This study investigates the influence of restoration age, landscape context, intrinsic site conditions and vegetation structure on the biodiversity and functional recovery of restored forests that have the same land-use history but differ in the year of planting (2-17 years). This study also assesses the relative influence of environmental factors potentially under the control of restoration efforts (vegetation structure, microhabitat conditions) compared with independent factors that would need to be accounted for at the pre-restoration planning phase (landscape context, soil characteristics).
- Overall, biodiversity and ecosystem functionality increased with restoration age, and communities became more similar to those of rainforest. In terms of vegetation structure, restoration led to sites becoming more structurally complex and similar to rainforest with age. Microhabitats were more complex and microclimatic conditions were more stable in restored sites and became more similar to rainforest with age. Soil properties and landscape context variables were unaffected by restoration age.
- Both mammal and dung beetle diversity recovery was best explained by vegetation structure and microhabitat conditions, exhibiting little response to landscape context or soil properties. Functional recovery, however, was best explained by a combination of both restoration dependent and independent factors: vegetation structure, microhabitat, soil properties and landscape context.
- *Synthesis and Applications.* These findings suggest that although landscape context and intrinsic site characteristics affect restoration success, they can potentially be mitigated to a degree by the establishment of a well-developed, rainforest-like habitat structure and microclimatic conditions within the restoration site. This study also indicates that biodiversity and functional recovery is influenced by the interaction of factors at multiple spatial scales from the microsite to the landscape and that higher order factors impose constraints at

lower levels. Therefore, it is important that restoration practitioners and land managers account for landscape context and pre-restoration site conditions when making decisions on when and how to restore tropical forests.

Keywords: ecosystem functioning; ecological restoration; functional diversity; decomposition; mammals; dung beetles; reforestation; landscape context; biodiversity; tropical forest; wet tropics

5.2 INTRODUCTION

Ecological restoration is an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability (SER ISPWG 2004). A major goal of ecological restoration is the re-establishment of the characteristics of an ecosystem, such as biodiversity and ecological function, that were prevalent before degradation (Jordan et al. 1990). It has been suggested that assessments of three major ecosystem attributes should be used to evaluate restoration success: diversity; vegetation structure; and ecological processes (Ruiz-Jaen and Aide 2005). However, studies on the success of ecological restoration have focussed largely on the recovery of vegetation structure and floral species diversity (Brudvig 2011), with little research conducted on other attributes until relatively recently (Majer 2009). In addition, the inclusion of landscape context attributes have been recommended when determining whether the goal of restoration has been accomplished (SER ISPWG 2004). Although landscape context is generally addressed in the initial planning stages of restoration, its contribution to the success or failure of restoration is rarely investigated.

The success of restoration plantings depends on a myriad of ultimate (indirect) and proximate (direct) variables operating simultaneously across multiple spatial scales (Arroyo-Rodríguez et al. 2015). Even in a single forest type within a region, successional recovery may follow divergent pathways, resulting in the success or failure of restoration projects (Mesquita et al. 2001, Norden et al. 2011, Cole et al. 2014, Jakovac et al. 2015, Norden et al. 2015). Recovery of communities and functions following ecological restoration is highly variable, with pathways strongly influenced by a number of potential environmental and ecological filters (Uhl et al. 1988, Holl 1999, Walker et al. 2010). Recently, Crouzeilles et al. (2016) identified three main ecological drivers of forest restoration success at the local and landscape scale: the time elapsed since restoration began, disturbance history and landscape context. Landscape context is an important factor implicated in the recovery of restored forests. The extent, intactness and configuration of nearby mature forest affects succession (Holl 1999, Guariguata and Ostertag 2001, Sloan et al. 2016), limiting the pool of propagules available for dispersal via wind or fauna (Uhl et al. 1988, Holl et al. 2000). Furthermore, it is widely documented that the amount and spatial configuration of habitat at the landscape level plays a key role in the persistence of faunal species (Fahrig 2003, Lindenmayer et al. 2006, Beukema et al. 2007, Bowen et al. 2007, Holl 2007, Chazdon et al. 2009a).

Local factors, including abiotic gradients, including rainfall, temperature, and soil type also influence the rate of recovery in tropical forests (Holl 2007). Intrinsic site conditions such as soil fertility and topography can have strong influences on vegetation growth rates and thus successional recovery (Herrera and Finegan 1997, Moran et al. 2000, Zarin et al. 2001), yet are rarely addressed in restoration studies.

The rate and direction of forest recovery are also influenced by past land use history, particularly previous anthropogenic land use (Moran et al. 2000, Jones and Schmitz 2009). The intensity and duration of past land use affects many site-specific factors that influence the rate of recovery (reviewed in Holl 2007), including the availability of propagules within a site (Holl 2007), availability of remnant vegetation (Saunders et al. 1991; reviewed in Holl and Cairns Jr 2002), soil properties (Reiners et al. 1994, Holt et al. 1996) and hydrology (Li et al. 2007, Zimmerman et al. 2007).

Previous research has shown that time since restoration began (or ‘restoration age’) is a key factor in explaining restoration success of biodiversity and vegetation structure in forests (Dunn 2004, Martin et al. 2013, Cole et al. 2014, Curran et al. 2014, Crouzeilles et al. 2016). Yet these studies often analyse restoration age only (Guariguata and Ostertag 2001, Chazdon 2003, 2008a, 2014, Arroyo - Rodríguez et al. 2015, Lohbeck et al. 2015), ignoring other potential drivers and thus fail to assess (nor control for) the effects of other key variables that can shape successional pathways and ecosystem recovery. By including a variety of key multi-scale factors into study models, restoration assessments can potentially identify the most important drivers of success (Arroyo-Rodríguez et al. 2015, Crouzeilles et al. 2016).

As such, this work addresses these key knowledge gaps by investigating the influence of restoration age, landscape context, intrinsic site conditions and vegetation structure on the biodiversity and functional recovery of restored forests that have the same land-use history. This work aims to determine the key drivers of restoration success by assessing the relative influence of environmental factors potentially under the control of restoration efforts (vegetation structure, microhabitat conditions) compared with independent factors that would need to be accounted for at the pre-restoration planning phase (landscape context, soil characteristics). More specifically, this study examines: (1) how biophysical parameters (vegetation structure, microhabitat conditions, soil properties and landscape context) respond to ecological restoration; (2) the effect of biophysical parameters on biodiversity and ecosystem functioning; and (3) whether restoration-dependent characteristics (i.e. vegetation structure, microhabitat conditions) are more important than restoration-independent characteristics (i.e. soil properties, landscape context) in driving patterns of biodiversity and functionality recovery.

5.3 MATERIALS AND METHODS

5.3.1 Study area

The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-elevation (500-1000 m) plateau in north-east Queensland, Australia (approximately 17°- 17°30’ S, 145°30’- 145°45’ E). The climate is predominantly humid tropical with temperatures of 15.6°C – 25.3°C (Bureau of Meteorology 2016) and rainforests are mostly complex notophyll to mesophyll vine-forest (Stanton and Stanton 2005). Most rainforests on the Tableland were cleared for agriculture 80 - 100 years ago, although small patches of remnant rainforest remain, and large (>3,000 ha) tracts of unfragmented rainforest survive on steeper hillsides. In recent decades there has been an expansion of rainforest restoration projects, with a high diversity (10 - 100+ species) of native rainforest trees and shrubs planted at high densities (ca. 3000 - 6000 stems/ha), in small (<5 ha) patches and strips, mainly in riparian areas (Goosem and Tucker 2013). The resulting landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant rainforest, natural regrowth and replanted forests.

5.3.2 Study design

Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years (n=1). These restoration sites were categorised into young (1-5 years), mid-age (6-12 years) and old (13-17 years) restoration categories. All restoration sites were previously grazed pasture. Remnant rainforest patches were considered as the reference target sites, representing the desired end point of restoration (n=4) and ungrazed, abandoned (for between 3 and 10 years) pasture on previously cleared rainforest land as the reference degraded sites (n=4), representing the starting point of restoration. Sample sites were set up in four blocks within the landscape, with each block containing one site of each of the three restoration categories and starting and reference sites: pasture; young restoration planting; mid-age restoration planting; old restoration planting; and rainforest. Blocks were selected to represent the maximum variation in topographic, climatic and geological parameters in the landscape so all sites within a block were similar in these parameters. Sites were separated by >300 m and blocks by >1.5 km. All restoration and degraded pasture sites were of similar size and shape (1 – 4 ha) and were 200 – 1000 m from intact rainforest, connected through restored and remnant corridors. All rainforest reference sites were at least 300 ha in size. A 50m x 20m study plot was established in the centre of each site, within which all sampling took place.

5.3.3 Ecosystem functions

To examine *in situ* leaf-litter decomposition, the litterbag method was used (Bocock and Gilbert 1957, Singh and Gupta 1977, Harmon et al. 1999), described in chapter four. Litterbags were laid out on the forest floor in arrays of eight litterbags, with two arrays placed at each study plot, at 5m and 45m along the centre line of the plot. The proportions of mass, carbon, nitrogen and phosphorus lost from the litterbags were determined through chemical analysis. Three dung beetle functions considered important to recovering forests - dung removal, secondary seed dispersal and soil excavation, were measured using four experimental dung baits set up 10 m apart along the centre line at each study plot (for detailed methods see chapter three; Derhé et al. 2016). Dung beetle functional experiments were conducted during the wet season in January - February 2014. A decomposition multifunctionality variable (sensu Mouillot et al. 2013) was calculated as the mean value of dung removed and mass lost from litter-bags, after standardizing each function (mean of 0 and standard deviation of 1) in order to give them the same weight. This multifunctionality variable provides a measure of functionality in both dung and leaf litter decomposition pathways.

5.3.4 Biodiversity sampling

Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) sampling was conducted twice during the wet season: January - February and May - June 2014 using four standardised baited pitfall traps (Spector and Forsyth 1998) 10 m apart along the centre line of each study plot (see chapter three; Derhé et al. 2016). Mammal sampling was conducted over a consecutive three day/ three night period (Tasker and Dickman 2002) on four separate occasions at each site, covering both the wet (Feb-Mar 2014 and Feb-Mar 2015) and dry season (Sept-Oct 2013 and Sept-Oct 2014). Mammal trapping occurred in a 50 m × 10 m transect within each study plot, using a combination of baited wire cage traps and Elliott A box traps (see description in chapter two).

Dung beetle and mammal species were characterised in terms of several main functional criteria that were considered relevant to their contribution to ecosystem functions within regenerating forests (see Supplementary material and, chapter two and three for more details). The "FD" package for R was used to calculate four complementary measures of functional diversity which describe a different functional aspect of biological communities: (1) functional richness (FRic); (2) functional evenness (FEve); (3) functional divergence (FDiv) (Villéger et al. 2008); and (4) functional dispersion (FDis) (Laliberté and Legendre 2010). Functional diversity metrics were calculated for mammals and dung beetle communities separately.

5.3.5 Biophysical characteristics

A number of biophysical variables related to ecological succession were quantified for each site, and were split into vegetation structure, microhabitat conditions, soil properties and landscape context. These variables were selected based on their potential to influence rainforest floral and faunal communities in the Wet Tropics (Wardell-Johnson et al. 2001, Kanowski et al. 2003, Catterall et al. 2004, Kanowski et al. 2006), particularly small-mammal (Laurance 1994, Williams and Marsh 1998) and dung beetle assemblages (Horgan 2005, Grimbacher et al. 2006, Grimbacher and Catterall 2007, Nichols et al. 2007), and leaf litter decomposition rates (Cenciani et al. 2009, Cusack et al. 2009, Powers et al. 2009a). Biophysical variables which are indicative of the successional pathway of regenerating forests (Kanowski et al. 2003, Lamb and Gilmour 2003, Kanowski and Catterall 2007, Kanowski et al. 2009, Kanowski et al. 2010) were also measured. These were: canopy cover and height; understory shrub cover; grass cover; basal area of live and dead trees; leaf and woody litter volume; ground temperature and humidity. In addition, site characteristics which are likely to be unaffected by restoration were measured: soil pH and bulk density, amount of nitrogen, carbon, total phosphorus and plant-available phosphorus in the soil; distance to nearest intact rainforest and pasture; area of study site; and percentage of forest cover within a 250m buffer of the study plot. All habitat measurements were taken within the 50m x 20m study plot in the centre of each site.

Canopy cover was measured from hemispherical photographs taken using a fisheye hemispherical lens and analysed with the software Gap Light Analyzer 2.0 (Frazer et al. 1999). The canopy was photographed from the understory (camera oriented towards the sky), to produce a circular image of the canopy. The software then transforms the colours from hemispherical photos to black and white, in order to quantify the number of pixels of the photograph corresponding to canopy. Canopy cover is then calculated as the proportion of the total number of black pixels in the photograph. To determine the proportion of canopy cover of each site, four canopy photographs were taken at 10m, 20m, 30m and 40m along the centre line of the study plot within each study site and the mean was calculated. Canopy height within each study plot was calculated by measuring the height of the tallest tree visible on the centre line using a digital clinometer. To calculate the mean canopy height of each site, four measurements were taken at 10m, 20m, 30m and 40m along the centre line of the study plot within the site.

Understory shrub cover was measured by photographing the understory shrub layer using a black sheet (1 x 1 m) arranged perpendicularly to the ground as background. A normal camera lens was used and the camera was positioned 3 m away from the background. A total of 8 photographs were taken along the central line of the study plot within a site, at 5m, 10m, 20m, 30m and 40m either side of the centre point of central line. The photographs were then analysed with the software Sidelook 1.1 (Nobis 2005) and the mean value calculated. This software converts the photographs into polarised black and white pictures, providing the percentage of black (vegetation) and white (no vegetation) pixels and provides a measure of both percentage cover and indices of vegetation complexity. Understory grass cover was calculated in the same way.

The total basal area of trees within each study plot was calculated by making counts of all free-standing woody-stemmed plants that were taller than 1m above the soil, recorded by DBH (diameter at breast height), following Kanowski et al (2010). The total basal area was calculated as the sum of the basal area of all woody-stemmed plants recorded within the study plot (in m ha^{-2}). Basal area for live trees and standing dead trees were calculated separately.

Woody litter and leaf litter volume were measured within three 50cm x 50cm quadrats placed at 5m, 25m and 45m along the centre line of the study plot. All woody litter and leaf litter from within the quadrat was collected and all topsoil removed, before the litter was oven-dried at 60°C until a constant weight was achieved. Mean woody and leaf litter volume was calculated for each site from the dry mass of woody litter and leaf litter for each quadrat. Temperature and humidity were recorded during the study period (October 2013 – April 2014) using Hygrochron iButton® data-loggers, with one logger at the centre of each study plot, beneath the leaf litter layer, which recorded hourly temperature and humidity to 0.1°C. The mean and coefficient of variation (as a measure of variability) were calculated from the temperature and humidity data collected and used for the analysis.

Two soil cores (30 mm diameter x 10cm depth) were collected in April 2014 at 5m and 45m along the centre line of the study plot. Subsamples of each soil core were oven-dried at 60°C and analysed for percentage carbon and percentage nitrogen on an Elementar Vario EL elemental analyser (Hanau, Germany), and for total phosphorus (using the Kjedahl digestion method) and plant-available phosphorus concentration (using the Olsen method) with an autoanalyser (Anderson and Ingram 1989). All stones and roots were removed and the soil samples were dried at 60°C until a constant weight was achieved, then weighed. A sub-sample of the dried soil was re-wetted and analysed for pH using a pH meter. Soil bulk density (g cm^{-3}) was calculated from the oven-dry mass of the 30 mm x 100 mm soil cores, minus the volume of any stones and coarse roots removed from the samples.

Area of study site, and distance to nearest intact rainforest and pasture and the percentage of intact rainforest cover within a 250m buffer of each study site was calculated in Q-GIS using a vegetation classification layer combined with georeferenced of aerial photographs (1:100.000) provided by CSIRO, Australia. Elevation and slope angle were calculated from the CSIRO Digital Elevation model dataset using QGIS. Distance to nearest intact rainforest was considered as a proxy of distance to species source pools.

5.3.6 Data analysis

Statistical analyses were carried out using R version 3.1.1 (R Core Team 2014). To test for correlations amongst biophysical parameters, biodiversity and functionality metrics, Pearson's product moment correlation coefficient was used. To test for effects of restoration age and habitat category on biophysical parameters, biodiversity and ecosystem functions, generalized linear mixed effects models were used (glmms) with block as a random effect. The statistical significance of the predictor variable in each glmm was tested with analysis of variance (ANOVA). A contrast analysis on the glmms was performed, with habitat category as a predictor, by obtaining confidence intervals using parametric bootstrapping to determine whether the response variables differed among rainforest, pasture and restoration categories. Appropriate error structures were applied for all models (Table S1).

Since biophysical variables were correlated, Principal Component Analysis (PCA, Gaunch 1984) was chosen to minimise the effects of multicollinearity before assessing the contribution of these biophysical variables on the response variables (diversity and functionality metrics)(Legendre and Legendre 1998). Since PCA axes are, by definition, orthogonal and independent of one another, this procedure creates composite, independent, environmental variables and avoids the danger of spurious correlations (Voigt et al. 2003). Prior to PCA modelling, biophysical parameters were transformed to meet the assumptions of normality (where possible) and standardised to have a mean of 0 and standard deviation of 1 (z-transformation). The first four PCA axes explained 81.0% of the total variance in the original data, so to investigate relationships between response variables (biodiversity and functionality) and biophysical parameters, glmms were performed, using these first four PCA axes. An information-theoretic approach was used to evaluate the relationships between the biodiversity and functionality metrics and the first four PCA axes. Each model was comprised with landscape ‘block’ as the random effect and appropriate error structures were applied for all models. All combinations of the full model and predictor variables (PCs 1:4) were run using the *MuMIn* package in R (Bartoń 2016). The Akaike’s Information Criterion corrected for small sample size (AIC_c) was used to evaluate models, by comparing the differences in AIC_c for each model with respect to the AIC_c of the best candidate model (Burnham and Anderson 2002). Based on the relative likelihoods of the different models, Akaike weights (w_i) were calculated to determine the weight of evidence in favour of each model being the best model in the set of candidate models (Burnham and Anderson 2002).

5.4 RESULTS

5.4.1 Effect of restoration on biophysical parameters

Proportion of canopy cover ($\chi^2 = 5.04$, $P = 0.025$; Figure 5.1a), canopy height ($\chi^2 = 14.36$, $P < 0.001$; Figure 5.1b), proportion of understory shrub cover ($\chi^2 = 23.93$, $P < 0.001$; Figure 5.1c), basal area of live ($\chi^2 = 13.17$, $P < 0.001$; Figure 5.1e) and dead trees ($\chi^2 = 38.09$, $P < 0.001$; Figure 5.1f), mean humidity ($\chi^2 = 5.52$, $P = 0.019$; Figure 5.2b), leaf litter volume ($\chi^2 = 4.14$, $P = 0.042$; Figure 5.2e) and woody litter volume ($\chi^2 = 18.02$, $P < 0.001$; Figure 5.2f) all increased significantly with restoration age. Mean temperature ($\chi^2 = 12.86$, $P < 0.001$; Figure 5.2a), variability in temperature ($\chi^2 = 14.2$, $P < 0.001$; Figure 5.2c) and variability in humidity ($\chi^2 = 13.24$, $P < 0.001$; Figure 5.2d) all decreased with restoration age.

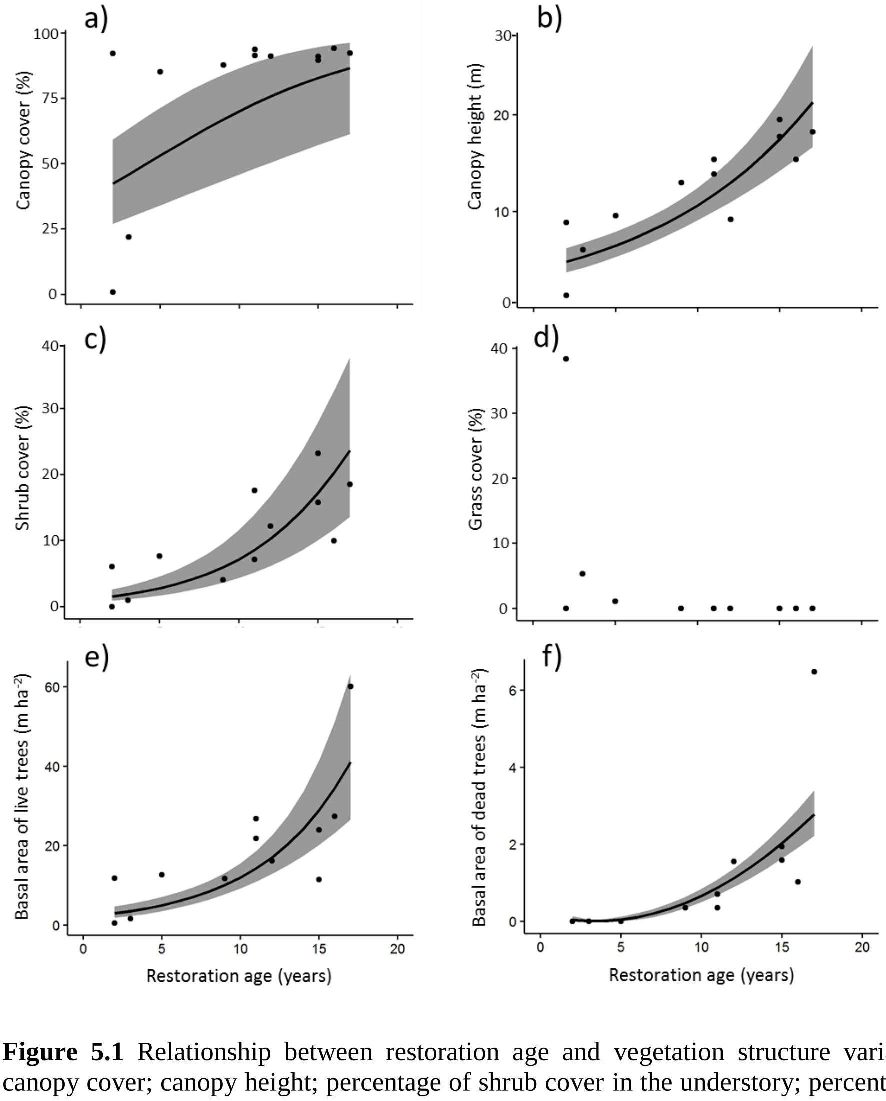


Figure 5.1 Relationship between restoration age and vegetation structure variables: percentage of canopy cover; canopy height; percentage of shrub cover in the understory; percentage of grass cover in the understory; basal area of live trees; and basal area of dead trees (a-f).

Proportion of grass cover (χ^2 = 3.00, P = 0.083; Figure 5.1d), soil pH (χ^2 = 2.54, P = 0.111; a), soil bulk density (χ^2 = 0.07, P = 0.792; Figure S5.7b), amount of carbon (χ^2 = 0.20, P = 0.658; Figure S5.7c), nitrogen (χ^2 = 0.09, P = 0.762; Figure S5.7d), total phosphorus (χ^2 = 0.16, P = 0.686; Figure S5.7e), plant-available phosphorus in the soil (χ^2 = 1.83, P = 0.176; Figure S5.7f), percentage of rainforest within a 250m buffer (χ^2 = 1.86, P = 0.172; Figure S5.8a), area of site (χ^2 = 0.01, P = 0.991; Figure S5.8b), distance to intact rainforest (χ^2 = 2.55, P = 0.110; Figure S5.8c), distance to pasture (χ^2 = 0.01, P = 0.908; Figure S5.8d), elevation (χ^2 = 1.27, P = 0.26; Figure S5.8e), and slope (χ^2 = 1.01, P = 0.314; Figure S5.8f) did not vary with restoration age.

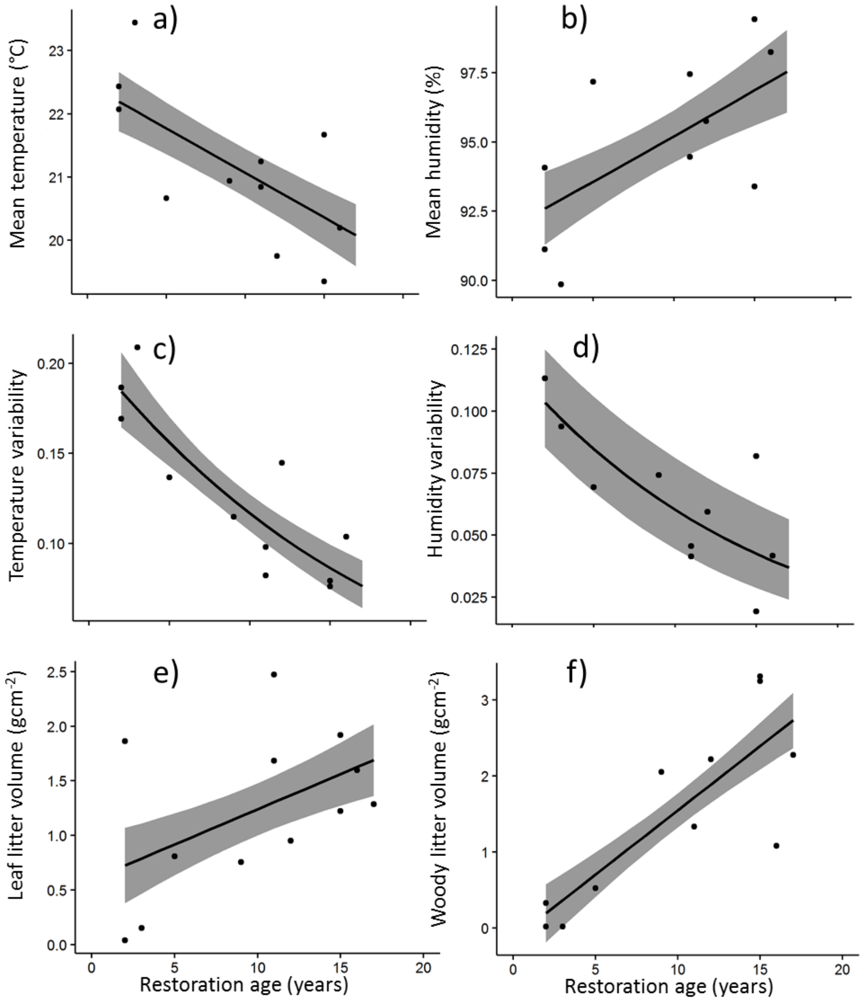


Figure 5.2 Relationship between restoration age and litter layer variables: mean temperature; mean humidity; temperature variability; humidity variability; leaf litter volume; and woody litter volume (a-f).

All vegetation structure parameters significantly differed among habitat categories (Table 5.1). Canopy cover, canopy height, understory shrub cover and basal area of live trees were all lower in pastures compared to any restoration and rainforest sites.

Young restoration sites had lower values than mid-age and old restoration sites and rainforest for all vegetation structure parameters, except for grass cover that was significantly higher in pastures but did not differ between the other habitat categories (Table 5.1). Rainforest had the highest value for all vegetation structure parameters, but did not differ from old restoration sites in terms of canopy height and understory shrub cover, or from mid age- and old restoration sites in terms of canopy cover and basal area of both live and dead trees. All microhabitat parameters, except for mean humidity, differed among habitat categories (Table 5.1). Mean temperature and variation in temperature and humidity were significantly higher in pasture and young reforestation sites than in mid age- and old reforestation sites and rainforest. Leaf and wood litter volume were significantly lower in pasture than any of the other habitat categories and were significantly higher in mid age- and old reforestation sites and rainforest compared to young reforestation sites (Table 5.1).

All soil parameters, except for phosphorous, significantly differed among habitat categories, with soil pH lower in rainforest and higher in pasture, soil bulk density lower in rainforest and pasture and higher in restoration sites, and percentage of C and N in the soil both higher in rainforest and lower in restoration sites (Table 5.1). Finally, several landscape context parameters (percentage of rainforest within a 250m buffer, area of site, distance to intact rainforest and distance to pasture) varied significantly by habitat category (Table 5.1) but these differences were independent of the habitat gradient (from pasture to rainforest). Several of the biophysical parameters relating to vegetation structure and microhabitat were highly correlated ($r > 0.70$; Figure S5.5); as were several of the soil properties and landscape context parameters ($r > 0.70$; Figure S5.5). In particular, canopy cover was positively correlated with canopy height ($r = 0.79$) and leaf litter volume ($r = 0.76$), and was negatively correlated with the proportion of grass cover ($r = -0.99$), mean temperature ($r = -0.81$) and variability in temperature ($r = -0.91$) and humidity ($r = -0.84$).

Table 5.1 Mean ± SE biophysical parameters for each habitat category (from GLMM outputs): vegetation structure; microhabitat conditions; soil properties; and landscape context variables. Superscripts represent pairwise differences at the P ≤ 0.05 level.

Biophysical parameter	Pasture	Young restoration	Mid-age restoration	Old restoration	Rainforest	χ^2	*P*
Vegetation structure							
Canopy cover (%)	2.50 ± 2.80^{a}	42.42 ± 20.49^{b}	81.10 ± 14.09^{c}	81.68 ± 13.78^{c}	84.98 ± 7.16^{c}	38.45	<0.001
Canopy height	0.64 ± 0.14^{a}	5.17 ± 1.12^{b}	12.64 ± 2.73^{c}	17.65 ± 3.82^{cd}	27.73 ± 6.00^{d}	55.64	<0.001
Understory shrub cover (%)	0.25 ± 0.23^{a}	1.16 ± 0.92^{b}	10.30 ± 4.43^{c}	17.49 ± 6.01^{cd}	27.15 ± 4.62^{d}	101.50	<0.001
Grass cover (%)	38.30 ± 13.62^{a}	3.44 ± 3.49^{b}	0.98 ± 1.11^{b}	0.98 ± 1.11^{b}	0.98 ± 0.72^{b}	31.31	<0.001
Basal area of trees	0.01 ± 0.01^{a}	3.37 ± 1.65^{b}	18.26 ± 8.93^{c}	25.93 ± 12.68^{c}	44.60 ± 21.81^{c}	197.17	<0.001
Basal area of dead trees	0^{a}	0^{a}	0.61 ± 0.15^{b}	2.13 ± 0.52^{c}	3.76 ± 0.92^{c}	197.50	<0.001
Microhabitat conditions							
Temperature variability†	0.24 ± 0.02^{a}	0.18 ± 0.02^{b}	0.11 ± 0.02^{c}	0.09 ± 0.02^{c}	0.08 ± 0.02^{c}	52.70	<0.001
Humidity variability†	0.15 ± 0.03^{a}	0.16 ± 0.03^{a}	0.05 ± 0.02^{b}	0.04 ± 0.02^{b}	0.06 ± 0.02^{b}	9.77	0.045
Mean temperature	22.78 ± 0.42^{a}	22.15 ± 0.42^{a}	20.70 ± 0.42^{b}	20.57 ± 0.45^{b}	20.16 ± 0.45^{b}	59.24	<0.001
Mean humidity	92.53 ± 2.21	93.02 ± 2.22	92.39 ± 2.21	96.61 ± 2.66	94.91 ± 2.61	2.39	0.665
Mean leaf litter (g cm^{-2})	0.02 ± 0.01^{a}	0.31 ± 0.13^{b}	1.31 ± 0.56^{c}	1.48 ± 0.64^{c}	1.68 ± 0.72^{c}	81.44	<0.001
Mean woody litter (g cm^{-2})	0.02 ± 0.01^{a}	0.09 ± 0.04^{a}	2.52 ± 1.17^{b}	2.27 ± 1.06^{b}	1.44 ± 0.67^{ab}	55.65	<0.001
Soil properties							
Soil pH	5.65 ± 0.10^{a}	5.33 ± 0.10^{b}	5.10 ± 0.10^{bc}	5.20 ± 0.10^{b}	4.83 ± 0.10^{c}	39.24	<0.001
Soil bulk density (g cm^{-3})	0.78 ± 0.06^{a}	0.94 ± 0.06^{b}	0.91 ± 0.06^{b}	0.97 ± 0.06^{b}	0.65 ± 0.06^{a}	26.25	<0.001
Soil C	6.84 ± 0.92^{ab}	5.38 ± 0.73^{a}	6.01 ± 0.81^{a}	5.59 ± 0.76^{a}	7.76 ± 1.05^{b}	11.87	0.018
Soil N	0.67 ± 0.05^{ab}	0.57 ± 0.05^{a}	0.60 ± 0.05^{a}	0.60 ± 0.05^{a}	0.74 ± 0.05^{b}	12.04	0.017
Soil total P	1.90 ± 0.67	2.097 ± 0.73	1.48 ± 0.52	1.95 ± 0.68	1.20 ± 0.42	2.91	0.574
Soil plant available P	0.24 ± 0.13	0.36 ± 0.19	0.29 ± 0.15	0.42 ± 0.22	0.21 ± 0.11	1.96	0.744
Landscape context							
% rainforest within 250m	2.88 ± 1.62^{ac}	18.77 ± 10.52^{b}	1.41 ± 0.79^{c}	8.41 ± 4.72^{ab}	92.36 ± 51.82^{d}	38.93	<0.001
Area (ha)	0.58 ± 0.23^{a}	0.26 ± 0.10^{a}	0.14 ± 0.05^{a}	0.31 ± 0.12^{a}	6.15 ± 2.45^{b}	57.44	<0.001
Distance to rainforest	114.92 ± 57.69^{a}	63.77 ± 32.01^{a}	747.02 ± 375.02^{b}	211.15 ± 106.00^{a}	0^{c}	63.58	<0.001
Distance to pasture	0^{a}	51.84 ± 15.71^{b}	55.84 ± 16.93^{b}	63.62 ± 19.29^{b}	411.07 ± 124.64^{c}	77.80	<0.001
Elevation (m)	857.77 ± 69.40	849.45 ± 68.73	788.59 ± 63.81	820.89 ± 66.42	839.37 ± 67.92	2.15	0.708
Slope (°)	3.90 ± 1.94	5.34 ± 2.66	3.05 ± 1.52	3.98 ± 1.99	7.32 ± 3.65	2.91	0.573

†Coefficient of variance

5.4.2 Effect of restoration on biodiversity and ecosystem functions

The response of biodiversity and ecosystem functions to restoration is reported in previous chapters. The direction and significance of the relationship between each response variable and restoration age and habitat category is summarised in Table 5.2. Decomposition multifunctionality increased with restoration age (χ^2 = 12.86, $P <$ 0.001; Figure 5.3a) and differed among habitat categories, with the lowest functionality in pasture and young restoration, and the highest in mid-age and old restoration and rainforest (χ^2 = 59.24, df = 4, < 0.001; Figure 5.3b). There was high correlation between the functional variables, with dung removal, seed dispersal and soil excavation being positively correlated (r > 0.70; Figure S5.6); and mean mass lost, nitrogen lost and carbon lost from litterbags being positively correlated (r > 0.70; Figure S5.6). There was positive correlation between the dung beetle diversity metrics: community similarity to rainforest, species richness, abundance, biomass and functional richness were all highly correlated with one another (r > 0.70; Figure S5.6). Mammal community similarity to rainforest was positively correlated with dung beetle species richness, dung beetle biomass, dung beetle functional richness and decomposition multifunctionality (r = 0.79; Figure S5.6). Mammal species richness and functional richness were positively correlated (r = 0.82; Figure S5.6), as were dung beetle species richness and mammal functional divergence (r = 0.70; Figure S5.6).

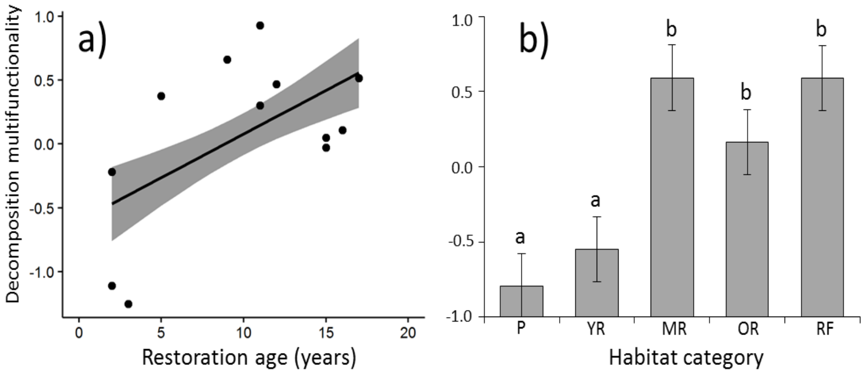


Figure 5.3 Relationship between restoration age and decomposition multifunctionality (a) and mean ± SE decomposition multifunctionality in the different habitat categories (b). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).

Table 5.2 Summary table of the responses of each biodiversity and functionality variable to restoration age and habitat category, and their respective significance values. P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest.

Response	**Effect of restoration age**	***P* (age)**	**Effect of habitat category** Lowest value	Highest value	***P* (category)**
Functionality					
Multifunctionality	+	<0.001	P; YR	MR; OR; RF	<0.001
Secondary seed dispersal	+	0.019	P; YR	RF	0.031
Dung removal	None	0.092	YR	P; MR; RF	0.009
Soil excavation	None	0.477	-	-	0.849
Mass lost from litterbags	+	0.018	P; YR	MR; OR; RF	<0.001
C lost from litterbags	+	0.045	P	YR; MR; OR	0.011
N lost from litterbags	None	0.090	P	YR; MR; OR	0.009
P lost from litterbags	None	0.572	-	-	0.205
Dung beetle diversity					
Similarity to rainforest	+	0.005	P; YR	MR; OR	<0.001
Species richness	+	<0.001	P; YR	RF	<0.001
Abundance	+	<0.001	P; YR	RF	<0.001
Biomass	+	0.011	P; YR	MR; OR; RF	<0.001
Functional richness	+	0.002	P; YR	OR; RF	<0.001
Functional evenness	–	0.004	-	-	0.178
Functional divergence	–	0.011	-	-	0.644
Functional dispersion	None	0.200	OR	RF	0.028
Mammal diversity					
Similarity to rainforest	+	0.007	P; YR	MR; OR	0.034
Species richness	None	0.997	-	-	0.755
Abundance	None	0.846	MR	P	0.029
Biomass	+	0.001	P	OR	0.003
Functional richness	None	0.303	-	-	0.557
Functional evenness	+	0.027	-	-	0.175
Functional divergence	None	0.279	MR	OR; RF	0.013
Functional dispersion	+	0.001	P	OR; RF	0.083

5.4.3 Effect of biophysical parameters on biodiversity and ecosystem functions

PCA axes were calculated for the original data of the twenty four biophysical parameters (Table 5.3). 65.3 % of the total variance in the original data was explained by the first two PCA axes, 45.6% by PC1 and 19.7 % by PC2. Axis 3 explained 8.2% and PC4 explained 7.4% of the total variance. Cumulatively PCs1 - 4 explained 81.0% of the total variance. Biplots showing the biophysical parameters, study sites and response variables are shown in Figure 5.4. PC1 primarily represents vegetation structure and microhabitat conditions that are influenced by restoration: canopy cover; canopy height; understory shrub cover; grass cover; basal area of live trees; basal area of dead trees; leaf litter volume; woody litter volume; mean temperature; temperature variability; humidity variability; soil pH; and distance to pasture (Figure 5.4 and Table 5.3). Conversely, PC2 primarily represents soil properties and landscape context parameters that are unaffected by restoration: soil bulk density; soil nitrogen, carbon and plant-available phosphorus; distance to intact rainforest; area of site; elevation; and slope (Figure 5.4 and Table 5.3). Thus, PC1 can be interpreted as representing habitat characteristics that demonstrate recovery with restoration; whereas PC2 can be interpreted as representing landscape and site variables that are independent of restoration.

Out of 24 biodiversity and functionality response variables modelled in relation to PCs 1:4, 14 response variables were found to be best explained by single or a combination of PCs (Table 5.4). For the remaining 10 response variables (dung removal, soil excavation, mammal species richness, mammal functional richness, mammal and dung beetle functional evenness divergence and dispersion), the null model was considered the best model based on AIC.

Table 5.3 The principal component coefficients (loadings) of the biophysical parameters for the four top PCA axes

Code	Biophysical parameter	PC1	PC2	PC3	PC4
CNC	Canopy cover (%)	-0.798	0.369	-0.075	0.028
CNH	Canopy height	-0.812	0.085	-0.283	-0.115
SHR	Understory shrub cover (%)	-0.899	0.054	-0.018	0.024
GRA	Grass cover (%)	0.736	-0.362	0.086	0.136
BAT	Basal area of trees	-0.843	0.157	-0.059	0.018
BAS	Basal area of dead trees	-0.831	-0.141	-0.106	-0.039
LLV	Mean leaf litter (g cm^{-2})	-0.763	0.272	0.090	0.119
WDV	Mean woody litter (g cm^{-2})	-0.705	0.375	0.273	0.118
TEM	Mean temperature	0.834	0.069	-0.074	-0.204
HUM	Mean humidity	-0.403	-0.118	0.188	0.307
TMV	Temperature variability†	0.833	-0.296	0.027	-0.032
HMV	Humidity variability†	0.755	-0.009	-0.333	-0.018
BLK	Soil bulk density (g cm^{-3})	0.259	0.730	-0.162	0.206
SPH	Soil pH	0.764	0.094	-0.039	0.001
SNI	Soil N	-0.299	-0.647	0.439	0.047
SCA	Soil C	-0.344	-0.655	0.458	0.098
STP	Soil total P	0.370	0.106	-0.207	0.517
PAP	Soil plant available P	0.189	0.486	-0.297	0.450
PRF	% rainforest within 250m	-0.492	-0.495	-0.447	-0.149
DRF	Distance to rainforest	0.046	0.727	0.414	0.036
DPA	Distance to pasture	-0.773	0.034	-0.332	0.016
SAR	Area (ha)	-0.280	-0.610	-0.404	-0.287
ELE	Elevation (m)	-0.105	-0.584	0.085	0.554
SLP	Slope (°)	-0.043	-0.459	-0.322	0.609

PC1 alone was considered the best model for 8 response variables (decomposition multifunctionality; secondary seed dispersal; dung beetle species richness, abundance, biomass and functional diversity; mammal similarity to rainforest and mammal biomass), PC2 alone was considered the best model for 2 response variables (C and N lost from litterbags), PC1 in combination with PC2 was considered the best model for 1 response variable only (mass lost from litterbags), while for the remaining 3 response variables (P lost from litterbags; dung beetle similarity to rainforest; mammal abundance) there was not sufficient evidence for a single best model ($\Delta \mathrm{AIC}_c < 2$) (Table 5.4). PC1 dominated the explanation of dung beetle and mammal diversity responses, whereas functionality responses were best explained by PC1 and PC2. PC3 did not feature as important in any model while PC4 featured in models for the 3 response variables without a single best model (Table 5.4).

Table 5.4 Support for generalized linear mixed models predicting ecosystem functioning and diversity in relation to the top four PCA components derived from the twenty-four biophysical parameters. Only response variables for which the top predictor(s) was not the null model are included in the table.

Response	**Predictor**	**log(L)**	**df**	**AIC**	**$\Delta \mathrm{AIC}_c$**	**w_i**	***P***
Functionality							
Decomposition multifunctionality	PC1	-12.48	4	36	0	0.81	<0.001
Secondary seed dispersal	PC1	0.15	4	10.8	0	0.58	0.002
Mass lost from litterbags	PC1 + PC2	19.64	5	-24.3	0	0.97	<0.001
C lost from litterbags	PC2	13.01	4	-14.9	0	0.72	<0.001
N lost from litterbags	PC2	13.19	4	-15.3	0	0.81	<0.001
P lost from litterbags	null model	10.92	3	-14.1	0	0.66	
	PC4	11.73	4	-12.4	1.74	0.28	0.006
Dung beetle diversity							
Dung beetle similarity to rainforest	PC1	36.92	4	-62.8	0	0.39	<0.001
	PC1+ PC4	38.29	5	-61.6	1.19	0.22	0.086
Dung beetle species richness	PC1	-44.05	4	99.2	0	0.57	<0.001
Dung beetle abundance	PC1	-97.81	4	206.7	0	0.62	<0.001
Dung beetle biomass	PC1	-152.80	4	316.7	0	0.65	<0.001
Dung beetle functional richness	PC1	-7.51	4	27.5	0	0.88	<0.001
Mammal diversity							
Mammal similarity to rainforest	PC1	10.47	4	-9.9	0	0.92	<0.001
Mammal abundance	PC1 + PC2	-70.57	5	156.1	0	0.31	0.020
	PC1	-72.99	4	157.1	0.93	0.19	0.027
	PC1 + PC4	-71.30	5	157.6	1.46	0.15	0.082
	PC2	-73.35	4	157.8	1.63	0.14	0.082
Mammal biomass	PC1	-19.11	4	49.3	0	0.45	0.009

* Block was included as a random effect in each model (n = 20 sites). log(L) is the log likelihood; df is the degrees of freedom; AICc is the Akaike's information criterion corrected for small sample size; ΔAICc is the difference in AICc compared to the best ranked model; w_i is the Akaike weight; and P-values designate the effect of each PCA component (or set of components) on the biodiversity or functional response variable.

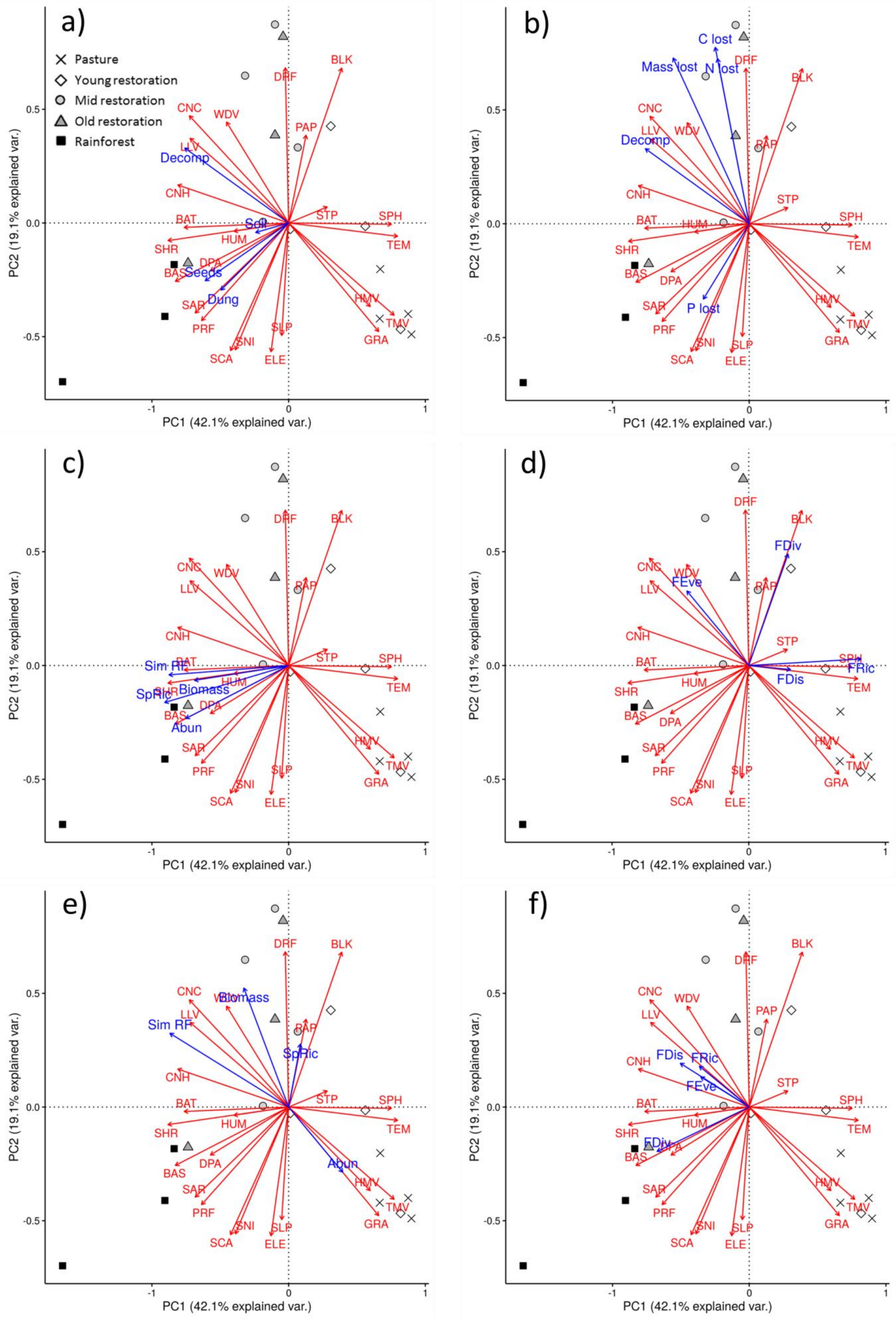


Figure 5.4 PCA-derived loadings plotted on the first two principal component axes for: dung beetle mediated functions (a); leaf litter decomposition (b); dung beetle species diversity (c); dung beetle functional diversity (d); mammal species diversity (e); and mammal functional diversity (f). Decomp = decomposition multifunctionality; dung = dung removal; soil = soil excavation; seeds = seed dispersal; Mass lost = mass lost from litterbags; N lost = nitrogen lost from litterbags; C lost = carbon lost from

litterbags; P lost = phosphorus lost from litterbags; Sim RF = community similarity to rainforest; SpRic = species richness; Abun = abundance; Biomass = total biomass; FRic = functional richness; FEve = functional evenness; FDiv = functional divergence; FDis = functional dispersion. CNC = canopy cover; CNH = canopy height; SHR = shrub cover; GRA = grass cover; BAT = basal area of trees; BAS = basal area of dead standing trees; BLK = soil bulk density; SPH = soil pH; SNI = soil nitrogen; SCA = soil carbon; STP = soil total phosphorus; PAP = soil plant-available phosphorus; LLV = leaf litter volume; WDV = woody litter volume; TEM = mean temperature; HUM = mean humidity; TMV = temperature variability; HMV = humidity variability; PRF = percentage of rainforest within 250m; DRF = distance to intact rainforest; DPA = distance to pasture; SAR = area of site; ELE = elevation; SLP = slope.

5.5 DISCUSSION

Overall, ecological restoration of tropical forests through direct planting of native tree species can be successful in facilitating the development of more rainforest-like habitat structure, increasing the availability of microhabitats and stabilising of microclimatic conditions. Consequently, this habitat development facilitates the recovery of native biodiversity and the reinstatement of ecosystem functions, and mitigates the effects of landscape effects such as isolation and fragmentation.

5.5.1 Effect of restoration on biophysical parameters

In terms of vegetation structure, restoration led to sites becoming more structurally complex and similar to rainforest with age. Older restoration sites had a high density of trees (higher basal area), a more closed canopy, taller trees, a denser shrub layer and more standing dead trees, in accord with other studies (Jennings et al. 1999, Kanowski et al. 2003). Canopy cover was relatively well established (>40%) in young restoration sites, becoming relatively ‘closed’ (>70%) at around five years since planting (Table 5.1; Figure 5.1a), corresponding with previous research in the study area (Kanowski et al. 2003, Nakamura et al. 2003, Grimbacher and Catterall 2007, Hobbs 2012, Goosem and Tucker 2013).

The canopy is a key regulator of abiotic conditions in the early stages of restoration and has a strong influence on other functionally important habitat attributes. Canopy structure affects light transmittance in the understory (Lieberman et al. 1989, De Steven 1994, Jones and Sharitz 1998) and so suppresses grass and weed growth through shading (Floyd 1990, Kooyman 1996), facilitating the establishment of rainforest understorey plants (Goosem and Tucker 1995, Kanowski et al. 2003). Indeed, this study found that increased canopy cover was correlated with decreased grass cover, a higher volume of leaf litter, lower temperatures and less variability in temperature and humidity. This further highlights the importance of establishing early canopy closure in restored plantings. Canopy closure has been considered a key component facilitating the development of fauna, especially during early stages of rainforest restoration (Jansen 1997, Nakamura et al. 2003, Kanowski et al. 2006, Grimbacher and Catterall 2007, Catterall et al. 2008).

In terms of microhabitat conditions, restored sites had a more complex microhabitat with a denser litter layer comprised of dead leaves and woody debris, similar to that of rainforest. The ground layer in restored sites was cooler, more humid and experienced fewer extremes in temperature and humidity than pastures, consistent with other studies (Chen et al. 1999, Jennings et al. 1999, Kanowski et al. 2003). For all vegetation structure and microhabitat condition variables, there was no difference between old restoration plantings and intact rainforest, demonstrating the effectiveness of restoration plantings in re-instating rainforest habitat structural and micro-climatic attributes.

None of the six soil properties measured here responded to restoration age, although soil pH, bulk density, carbon and nitrogen did vary by habitat category. This may be because the nutrient content and properties of soils in the Wet Tropics are known to be heavily influenced by geology (Teitzel and Bruce 1972, Spain 1990) and so may be less affected by short term changes in vegetation cover caused by restoration. Concentrations of carbon, total nitrogen, total phosphorus, soil pH can all vary with the type of bedrock, with soils derived from basalt having higher levels of these properties than those formed on other bedrock types (Spain 1990).

Landscape context metrics were independent from restoration in the present study. However, it is important to look at the effect of landscape context on restoration success as it is an often overlooked, yet key factor influencing successional recovery (Holl et al. 2000, Perfecto and Vandermeer 2008, Holl and Aide 2011).

5.5.2 Effect of restoration on biodiversity and functionality

Ecological restoration of previously forested pasture can enhance leaf litter decomposition rates and increase nutrient release from leaf litter back into the soil, increase dung beetle-mediated secondary seed dispersal, and improve decomposition multifunctionality. Tropical forest restoration can also recover rainforest-like communities of dung beetles and small mammals, and increase biomass and functional diversity of dung beetles and mammals in a relatively short time (10-17 years). These findings demonstrate that ecological restoration is an important strategy in mitigating biodiversity losses, reinstating functionality and recovering a degree of ecosystem stability in tropical forests. However, the outcome of restoration success depends on which ecological attribute is considered.

Several components of mammal diversity were highly correlated to dung beetle diversity; in particular, mammal community similarity to rainforest was positively correlated with several dung beetle diversity metrics, as well as decomposition multifunctionality. The availability of mammalian dung as a food resource is a key limitation to dung beetle reproduction and survival (Halffter and Edmonds 1982, Hanski and Cambefort 1991) and positive associations between mammals and dung beetles have been demonstrated in numerous studies (Estrada et al. 1998, Estrada et al. 1999, Nichols et al. 2009, Culot et al. 2013). The similarity of response and high correlation highlights the trophic link between mammals and dung beetles, and suggests that mammalian recovery could be indicative of the recovery of dung beetle communities in restored forests. However, these relationships could be idiosyncratic and further investigation is required to establish the causative nature of this relationship.

5.5.3 Effect of biophysical parameters on biodiversity

Biodiversity recovery was best explained by vegetation structure and microhabitat conditions (PC1; Table 5.4), exhibiting little response to landscape context or soil properties. Mammal diversity and the recovery of mammal biomass and community similarity to rainforest was most associated with an increase in the density of leaf litter, woody litter, canopy height and canopy cover, and a decrease in temperature and humidity variability (Figure 5.4e). This finding accords with previous studies which show that small mammal assemblage structure is closely related to vegetation structure, particularly canopy cover (Williams et al. 2002). This relationship is likely driven by the increase in availability of a variety of food and shelter resources that a dense litter and shrub layer and closed canopy provides for mammals, as well as stable microclimatic conditions (Dueser and Shugart 1978, Seagle 1985, Williams et al. 2002). Various other taxonomic groups in the study area have also demonstrated a preference for cooler, moist forest habitats, with an established litter layer and a stable microclimate, including reptiles (Kanowski et al. 2006, Shoo et al. 2014) and amphibians (Shoo et al. 2011).

Dung beetle diversity was predominantly influenced by PC1, indicating that vegetation structure and microhabitat are the most important determinants of dung beetle recovery (Table 5.4; Figure 5.4c). Recovery of dung beetle community similarity to rainforest, species richness, abundance and biomass was associated with a dense shrub layer, an increase in the density of both live and dead standing trees, and an increase in humidity. This finding is congruent with other studies which have shown that habitats with more complex, rainforest-like habitat conditions, including a high degree of canopy cover, dense shrub layer, and low variation in temperature and humidity have been shown to be associated with the development of rainforest invertebrate assemblages following reforestation (Jansen 1997, Nakamura et al. 2003, Grimbacher and Catterall 2007, Nakamura et al. 2009).

The recovery of dung beetle functional diversity appears to be a more complicated process, with each aspect of functional diversity being associated with different biophysical parameters, primarily soil and microhabitat conditions (Figure 5.4d). However, the best model prediction for most functional diversity metrics was the null model, which indicates that there are other more important explanatory factors influencing dung beetle functional diversity that were not measured in this study.

The restructuring of dung beetle communities following habitat change has been frequently explained by two non-exclusive hypotheses: changes in vegetation structure (Davis and Sutton 1998, Davis et al. 2002, Halffter and Arellano 2002) and changes in the availability of mammalian dung resources (Hanski and Cambefort 1991, Andresen 1999, Andresen and Laurance 2007, Coggan 2012). This demonstrates that although this study has revealed a close association between dung beetle community recovery and habitat conditions, there are likely to be additional factors driving this recovery that have not been investigated here – particularly the link between mammalian and dung beetle recovery.

5.5.4 Effect of biophysical parameters on ecosystem functions

Overall, the recovery of functionality appears to be driven by a combination of vegetation structure, microhabitat, soil properties and landscape context (PC1 and PC2; Table 5.4). Of these, vegetation structure and microhabitat conditions (PC1) were the best predictors of dung beetle mediated seed dispersal and decomposition multifunctionality; whereas leaf litter decomposition functions (mass, carbon and nitrogen lost from litterbags) were driven primarily by soil properties and landscape context (PC2).

High levels of decomposition multifunctionality (dung removal and litter mass lost combined) were most associated with increased litter volume and decreased variability in temperature and humidity (Figure 5.4a). Leaf litter decomposition was most associated with an increase in woody litter volume, canopy cover and distance to rainforest (Figure 5.4b). A closed canopy is a key regulator of abiotic conditions and provides a shaded forest floor which is associated with increased moisture content and reduced temperature fluctuations in soil and litter microhabitats (Neumann 1973, Goosem and Tucker 1995, Kanowski et al. 2003, Goosem and Tucker 2013), which all positively affect decomposition rates. A dense litter layer provides better insulation against temperature and moisture extremes, provides more food and habitat resources for colonising soil and litter arthropods and leads to greater microbial biomass and decomposition activity (Majer et al. 1984, Donnelly et al. 1990, Greenslade and Majer 1993, Nakamura et al. 2003).

The majority of dung decomposition is achieved by dung beetles, which breakdown and relocating dung, by consuming and metabolising it, and by facilitating the action of decomposing microbes (Hanski and Cambefort 1991). Fragment size and percentage of intact rainforest within a 250m buffer were found to be the most important drivers of dung removal in this study (Figure 5.4a). This indicates that dung beetles remove dung at a lower rate in smaller fragments and those surrounded by less rainforest than in larger ones with more surrounding rainforest. These results are supported by other tropical studies showing effects of fragmentation on dung beetle assemblage structure (Davis et al. 2001, Estrada and Coates-Estrada 2002, Scheffler 2005), and on the rate with which dung decomposes (Andresen 2003, Bustamante Sánchez et al. 2004, Larsen et al. 2005).

Microclimatic conditions, particularly temperature and humidity, are important for dung beetle-mediated processes too. In hot and dry conditions, dung becomes quickly unsuitable for most dung beetles as it becomes too desiccated (Hanski and Cambefort 1991), which limits dung decomposition and other related processes. Furthermore, canopy cover may also affect dung beetle activity directly (Young 1984), as some species are known to prefer perching on leaves that are located in sun flecks, likely to elevate body temperatures which aids foraging (Hanski and Cambefort 1991). However, dung beetles are also physiologically constrained by high temperatures, and so extremes of temperatures are likely to have negative effects on dung beetle activity (Verdú et al. 2006).

5.5.5 Conclusions

These findings provide strong evidence that ecological restoration plantings can facilitate forest succession through modification of both physical (e.g. temperature, humidity) and biological (e.g. canopy cover, denser litter layer) site conditions. Maximising mammal and dung beetle diversity comes from increasing the vegetation structural complexity and creating more stable, less hostile microclimatic conditions and microhabitats with a variety of food and shelter resources. Reinstating functionality through restoration requires incorporation of pre-restoration site conditions and landscape context, in addition to restoring habitat structure and creating stable microclimatic conditions.

The recovery of functionality appears to be a complex process which is driven by a combination of habitat structure and microclimate, along with landscape context and soil characteristics. The recovery of stable ecosystem functions requires multiple species, and often multiple, interacting functional groups, each of which have their own ecological requirements and responses to biophysical parameters. As such, the processes and parameters affecting ecosystem functional recovery will vary between the functions considered, and so restoration requirements of ecosystem functions should be considered on a case by case basis.

Landscape context appeared to have little effect on mammal and dung beetle diversity, which could be partly because all restoration sites in this study were connected through restored and remnant corridors, which provide linkages between forest areas for species movement and genetic interchange (Rosenberg et al. 1997, Lidicker Jr 1999, Levey et al. 2005, Paetkau et al. 2009) and thus partly reduce negative effects of isolation (distance from rainforest) and fragment size (Bennett 1990). Indeed, research in the study area reported the movement into and through a newly planted restoration corridor by small mammals, demonstrating population interchange and genetic flow across the corridor and between two previously isolated forest fragments (Paetkau et al. 2009, Tucker and Simmons 2009).

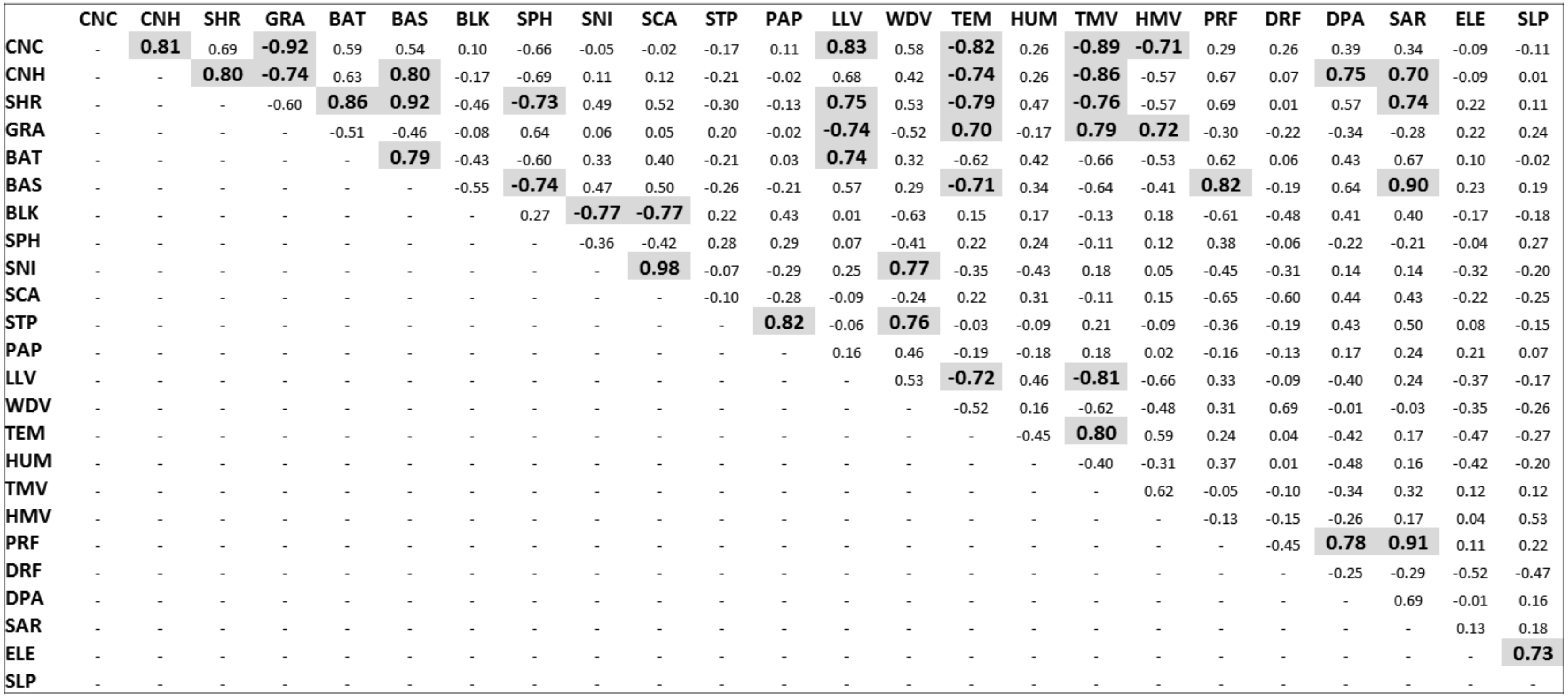
Additionally, the lack of effect of landscape context could potentially be because the minimum area requirements for these taxa are met by the habitat patches in this study. Other studies have demonstrated that small-bodied, highly mobile taxa, such as invertebrates, can persist in very small remnants (Abensperg-Traun and Smith 1999, Davies et al. 2001, Major et al. 2003, Driscoll and Weir 2005, Grimbacher et al. 2006). Previous research in the study area found that ground beetle abundance is unaffected by distance to rainforest, but is instead more influenced by vegetation structure (Grimbacher and Catterall 2007). In addition, it has been demonstrated that the effects of fragmentation are reduced for species with good dispersal ability (Driscoll and Weir 2005, Paetkau et al. 2009), and the influence of isolation on insect assemblages are small, relative to other effects (Thomas et al. 2001, Cunningham et al. 2005, Grimbacher et al. 2006). The findings from this study indicate that vegetation structure and microclimatic conditions could be mitigating landscape effects, including fragmentation and isolation, as suggested in previous studies (Grimbacher et al. 2006, Mérő et al. 2015).

It should also be noted that the reference rainforest sites used in this study are themselves fragmented to a degree, and therefore may suffer edge effects due to their relatively small size (≥300ha) (Ries et al. 2004, Harper et al. 2005). Nonetheless, in this situation, these forest fragments are a realistic target for restoration in the study area, since forest restoration at scales larger than these reference forest fragments is currently unfeasible in the study area (due to lack of marginal land, cost and availability of resources).

These findings demonstrate that although landscape context and intrinsic site characteristics affect restoration success, they can be mitigated to a degree by the establishment of a well-developed, rainforest-like habitat structure and microclimatic conditions within the restoration site. This study looks at the recovery of a small subset of ecosystem functions and faunal groups. The ecological drivers of restoration success have been shown to vary in magnitude of impacts among taxonomic groups and measures of vegetation structure. Since species differ in their dispersal ability (Paltto et al. 2006, Hedenås and Ericson 2008) and the scale at which they perceive the environment (Kotliar and Wiens 1990), patterns of recovery reported here may not necessarily represent those of less mobile organisms that are not able to disperse relatively long distances, or of larger-bodied taxa that require larger areas of habitat, or more landscape-dependent processes (e.g. stabilisation of hillslopes, and hydrological processes).

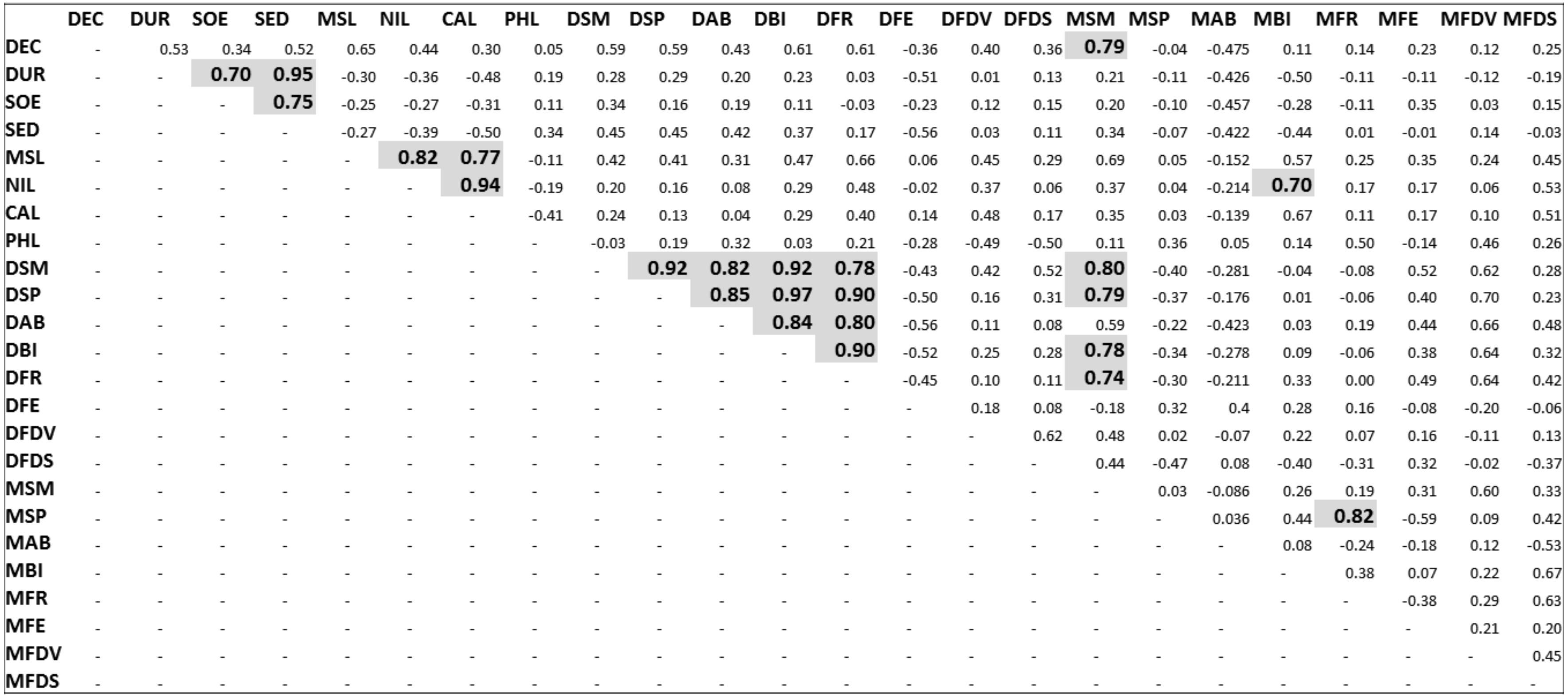
This study indicates that biodiversity and functional recovery is influenced by the interaction of factors at multiple spatial scales from the microsite to the landscape and that higher order factors impose constraints at lower levels. Therefore, it is important that restoration practitioners and land managers account for landscape context and pre-restoration site conditions when making decisions on when and how to restore tropical forests.

5.6 SUPPORTING INFORMATION



	CNC	CNH	SHR	GRA	BAT	BAS	BLK	SPH	SNI	SCA	STP	PAP	LLV	WDV	TEM	HUM	TMV	HMV	PRF	DRF	DPA	SAR	ELE	SLP
CNC	-	**0.81**	0.69	**-0.92**	0.59	0.54	0.10	-0.66	-0.05	-0.02	-0.17	0.11	**0.83**	0.58	**-0.82**	0.26	**-0.89**	**-0.71**	0.29	0.26	0.39	0.34	-0.09	-0.11
CNH	-	-	**0.80**	**-0.74**	0.63	**0.80**	-0.17	-0.69	0.11	0.12	-0.21	-0.02	0.68	0.42	**-0.74**	0.26	**-0.86**	-0.57	0.67	0.07	**0.75**	**0.70**	-0.09	0.01
SHR	-	-	-	-0.60	**0.86**	**0.92**	-0.46	**-0.73**	0.49	0.52	-0.30	-0.13	**0.75**	0.53	**-0.79**	0.47	**-0.76**	-0.57	0.69	0.01	0.57	**0.74**	0.22	0.11
GRA	-	-	-	-	-0.51	-0.46	-0.08	0.64	0.06	0.05	0.20	-0.02	**-0.74**	-0.52	**0.70**	-0.17	**0.79**	**0.72**	-0.30	-0.22	-0.34	-0.28	0.22	0.24
BAT	-	-	-	-	-	**0.79**	-0.43	-0.60	0.33	0.40	-0.21	0.03	**0.74**	0.32	-0.62	0.42	-0.66	-0.53	0.62	0.06	0.43	0.67	0.10	-0.02
BAS	-	-	-	-	-	-	-0.55	**-0.74**	0.47	0.50	-0.26	-0.21	0.57	0.29	**-0.71**	0.34	-0.64	-0.41	**0.82**	-0.19	0.64	**0.90**	0.23	0.19
BLK	-	-	-	-	-	-	-	0.27	**-0.77**	**-0.77**	0.22	0.43	0.01	-0.63	0.15	0.17	-0.13	0.18	-0.61	-0.48	0.41	0.40	-0.17	-0.18
SPH	-	-	-	-	-	-	-	-	-0.36	-0.42	0.28	0.29	0.07	-0.41	0.22	0.24	-0.11	0.12	0.38	-0.06	-0.22	-0.21	-0.04	0.27
SNI	-	-	-	-	-	-	-	-	-	**0.98**	-0.07	-0.29	0.25	**0.77**	-0.35	-0.43	0.18	0.05	-0.45	-0.31	0.14	0.14	-0.32	-0.20
SCA	-	-	-	-	-	-	-	-	-	-	-0.10	-0.28	-0.09	-0.24	0.22	0.31	-0.11	0.15	-0.65	-0.60	0.44	0.43	-0.22	-0.25
STP	-	-	-	-	-	-	-	-	-	-	-	**0.82**	-0.06	**0.76**	-0.03	-0.09	0.21	-0.09	-0.36	-0.19	0.43	0.50	0.08	-0.15
PAP	-	-	-	-	-	-	-	-	-	-	-	-	0.16	0.46	-0.19	-0.18	0.18	0.02	-0.16	-0.13	0.17	0.24	0.21	0.07
LLV	-	-	-	-	-	-	-	-	-	-	-	-	-	0.53	**-0.72**	0.46	**-0.81**	-0.66	0.33	-0.09	-0.40	0.24	-0.37	-0.17
WDV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.52	0.16	-0.62	-0.48	0.31	0.69	-0.01	-0.03	-0.35	-0.26
TEM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.45	**0.80**	0.59	0.24	0.04	-0.42	0.17	-0.47	-0.27
HUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.40	-0.31	0.37	0.01	-0.48	0.16	-0.42	-0.20
TMV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.62	-0.05	-0.10	-0.34	0.32	0.12	0.12
HMV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.13	-0.15	-0.26	0.17	0.04	0.53
PRF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.45	**0.78**	**0.91**	0.11	0.22
DRF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.25	-0.29	-0.52	-0.47
DPA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.69	-0.01	0.16
SAR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.13	0.18
ELE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0.73**
SLP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure S5.5 Associations (Pearson's ρ) between biophysical parameters: CNC = canopy cover; CNH = canopy height; SHR = shrub cover; GRA = grass cover; BAT = basal area of trees; BAS = basal area of dead standing trees; BLK = soil bulk density; SPH = soil pH; SNI = soil nitrogen; SCA = soil carbon; STP = soil total phosphorus; PAP = soil plant-available phosphorus; LLV = leaf litter volume; WDV = woody litter volume; TEM = mean temperature; HUM = mean humidity; TMV = temperature variability; HMV = humidity variability; PRF = percentage of rainforest within 250m; DRF = distance to intact rainforest; DPA = distance to pasture; SAR = area of site; ELE = elevation; SLP = slope. Bold numbers indicate a strong correlation (Pearson's p ≥ 0.7) between variables.



	DEC	DUR	SOE	SED	MSL	NIL	CAL	PHL	DSM	DSP	DAB	DBI	DFR	DFE	DFDV	DFDS	MSM	MSP	MAB	MBI	MFR	MFE	MFDV	MFDS
DEC	-	0.53	0.34	0.52	0.65	0.44	0.30	0.05	0.59	0.59	0.43	0.61	0.61	-0.36	0.40	0.36	**0.79**	-0.04	-0.475	0.11	0.14	0.23	0.12	0.25
DUR	-	-	**0.70**	**0.95**	-0.30	-0.36	-0.48	0.19	0.28	0.29	0.20	0.23	0.03	-0.51	0.01	0.13	0.21	-0.11	-0.426	-0.50	-0.11	-0.11	-0.12	-0.19
SOE	-	-	-	**0.75**	-0.25	-0.27	-0.31	0.11	0.34	0.16	0.19	0.11	-0.03	-0.23	0.12	0.15	0.20	-0.10	-0.457	-0.28	-0.11	0.35	0.03	0.15
SED	-	-	-	-	-0.27	-0.39	-0.50	0.34	0.45	0.45	0.42	0.37	0.17	-0.56	0.03	0.11	0.34	-0.07	-0.422	-0.44	0.01	-0.01	0.14	-0.03
MSL	-	-	-	-	-	**0.82**	**0.77**	-0.11	0.42	0.41	0.31	0.47	0.66	0.06	0.45	0.29	0.69	0.05	-0.152	0.57	0.25	0.35	0.24	0.45
NIL	-	-	-	-	-	-	**0.94**	-0.19	0.20	0.16	0.08	0.29	0.48	-0.02	0.37	0.06	0.37	0.04	-0.214	**0.70**	0.17	0.17	0.06	0.53
CAL	-	-	-	-	-	-	-	-0.41	0.24	0.13	0.04	0.29	0.40	0.14	0.48	0.17	0.35	0.03	-0.139	0.67	0.11	0.17	0.10	0.51
PHL	-	-	-	-	-	-	-	-	-0.03	0.19	0.32	0.03	0.21	-0.28	-0.49	-0.50	0.11	0.36	0.05	0.14	0.50	-0.14	0.46	0.26
DSM	-	-	-	-	-	-	-	-	-	**0.92**	**0.82**	**0.92**	**0.78**	-0.43	0.42	0.52	**0.80**	-0.40	-0.281	-0.04	-0.08	0.52	0.62	0.28
DSP	-	-	-	-	-	-	-	-	-	-	**0.85**	**0.97**	**0.90**	-0.50	0.16	0.31	**0.79**	-0.37	-0.176	0.01	-0.06	0.40	0.70	0.23
DAB	-	-	-	-	-	-	-	-	-	-	-	**0.84**	**0.80**	-0.56	0.11	0.08	0.59	-0.22	-0.423	0.03	0.19	0.44	0.66	0.48
DBI	-	-	-	-	-	-	-	-	-	-	-	-	**0.90**	-0.52	0.25	0.28	**0.78**	-0.34	-0.278	0.09	-0.06	0.38	0.64	0.32
DFR	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.45	0.10	0.11	**0.74**	-0.30	-0.211	0.33	0.00	0.49	0.64	0.42
DFE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.18	0.08	-0.18	0.32	0.4	0.28	0.16	-0.08	-0.20	-0.06
DFDV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.62	0.48	0.02	-0.07	0.22	0.07	0.16	-0.11	0.13
DFDS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.44	-0.47	0.08	-0.40	-0.31	0.32	-0.02	-0.37
MSM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-0.086	0.26	0.19	0.31	0.60	0.33
MSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.036	0.44	**0.82**	-0.59	0.09	0.42
MAB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-0.24	-0.18	0.12	-0.53
MBI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.38	0.07	0.22	0.67
MFR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.38	0.29	0.63
MFE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.21	0.20
MFDV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.45
MFDS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure S5.6 Associations (Pearson's ρ) between biodiversity and functionality parameters: DEC = decomposition multifunctionality; DUR = dung removal; SOE = soil excavation; SED = seed dispersal; MSL = mass lost from litterbags; NIL = nitrogen lost from litterbags; CAL = carbon lost from litterbags; PHL = phosphorus lost from litterbags; DSM = dung beetle community similarity to rainforest; DSP = dung beetle species richness; DAB = dung beetle abundance; DBI = dung beetle biomass; DFR = dung beetle functional richness; DFE = dung beetle functional evenness; DFDV = dung beetle functional divergence; DFDS = dung beetle functional dispersion; MSM = mammal community similarity to rainforest; MSP = mammal species richness; MAB = mammal abundance; MBI = mammal biomass; MFR = mammal functional richness; MFE = mammal functional evenness; MFDV = mammal functional divergence; MFDS = mammal functional dispersion. Bold numbers indicate a strong correlation (Pearson's p ≥ 0.7) between variables.

Table S5.5 Structure of generalised linear mixed models for determining the effects of restoration age and habitat category on habitat and environmental variables

	Fixed effect: Restoration age		**Fixed effect: Habitat category**	
Response variable	**Error distribution**	**Transformation**	**Error distribution**	**Transformation**
Microclimate conditions				
Mean temperature	Gaussian		Gaussian	
Mean humidity	Gaussian	log(10)	Gaussian	log(10)
Temperature variability	Binomial (logit)		Binomial (logit)	
Humidity variability	Beta		Beta	
Woody litter volume	Gaussian	log(10)	Gaussian	log(10)
Leaf litter volume	Negative binomial		Gaussian	log(10)
Vegetation structure				
Canopy cover	Beta		Beta	
Canopy height	Gaussian	log(10)	Gaussian	log(10)
Understory shrub cover	Beta		Beta	
Grass cover	Binomial		Beta	
Basal area of trees	Gaussian	log(10)	Gaussian	log(10)
Basal area of dead stags	Gaussian	sqrt	Gaussian	log(10)
Soil properties				
Soil pH	Gaussian		Gaussian	
Soil bulk density	Gaussian		Gaussian	log(10)
Soil C	Gaussian		Gaussian	log(10)
Soil N	Gaussian		Gaussian	
Soil total P	Gaussian	log(10)	Gaussian	log(10)
Soil plant available P	Gaussian		Gaussian	log(10)
Landscape context				
% rainforest within 250m	Beta		Beta	
Area (ha)	Gaussian		Gaussian	log(10)
Distance to rainforest (m)	Gaussian	log(10)	Gaussian	log(10)
Distance to pasture (m)	Gaussian	log(10)	Gaussian	log(10)
Elevation (m)	Gaussian	log(10)	Gaussian	log(10)
Slope (°)	Gaussian	log(10)	Gaussian	log(10)

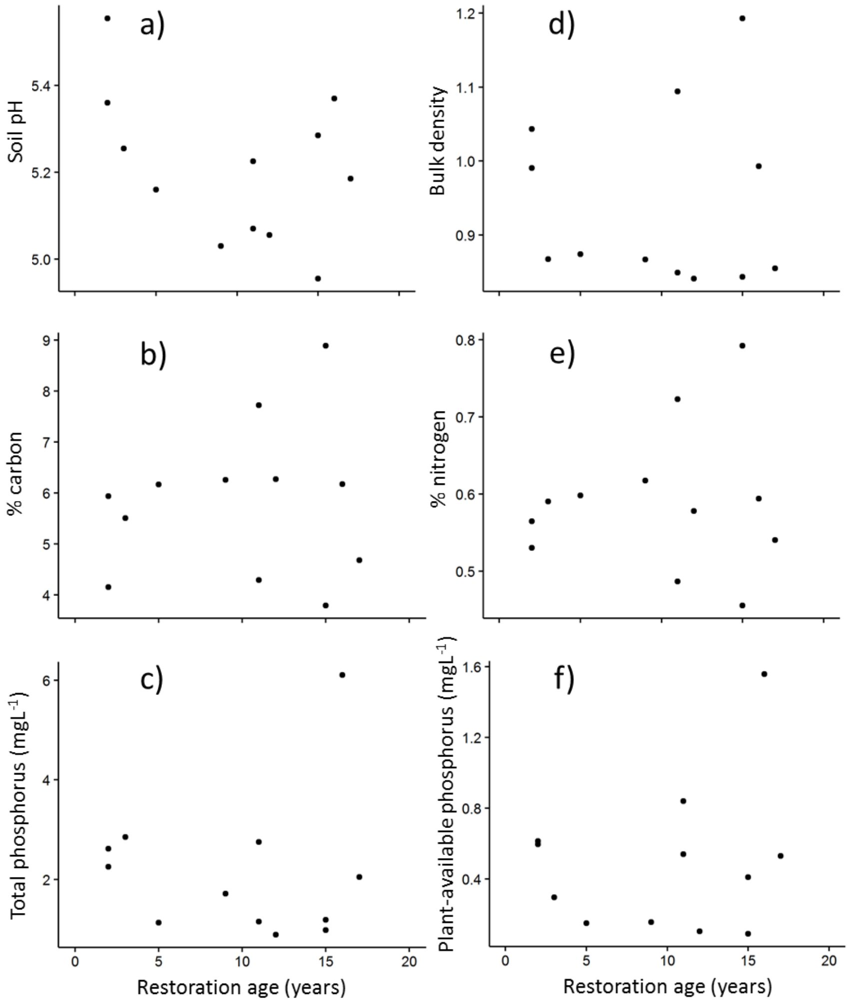


Figure S5.7 Relationship between restoration age and soil properties; soil pH; percentage of carbon in the soil; amount of total phosphorous in the soil (mgL^{-1}); soil bulk density; percentage of nitrogen in the soil; amount of plant-available phosphorous in the soil (mgL^{-1}) (a-f).

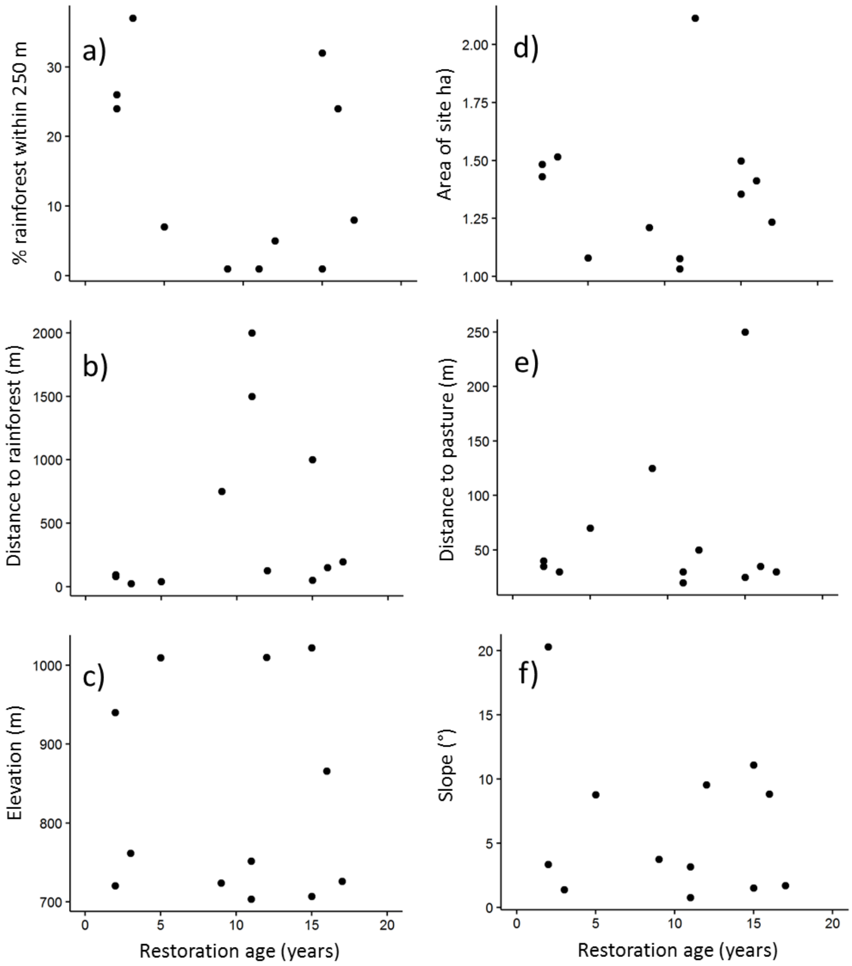


Figure S5.8 Relationship between restoration age and landscape context variables: % rainforest within a 250 m buffer; Distance to intact rainforest (m); Elevation (m); Area of site (ha); Distance to pasture (m); slope (°) (a-f).

Chapter 6

General discussion

6.1 GENERAL DISCUSSION

Tropical forests are disappearing rapidly, leading to major declines in tropical biodiversity (Pereira et al. 2010, Rands et al. 2010) and the disruption of important ecological functions and ecosystem services (Duffy 2009). Natural recovery of cleared forests is highly variable, with many ecosystems unable to recover without some form of human intervention. As such, ecological restoration is being increasingly applied to reverse or mitigate biodiversity losses, re-instate ecological functions and increase the provision of ecosystem services in tropical forests (Holl and Aide 2011). The overall aim of this thesis was to examine the effectiveness of ecological restoration in recovering tropical forest biodiversity and ecosystem functions, and to determine the key drivers of this recovery. In addressing this aim, a variety of diversity metrics were used to describe the recovery of two components of faunal diversity from different levels within a trophic system (chapters 2 and 3), whilst simultaneously assessing the recovery of important ecological functions relating to nutrient cycling (chapters 3 and 4) in a tropical forest system. The main drivers of these patterns of recovery were then investigated by examining the relative contribution of a range of biophysical parameters on each component of biodiversity and functionality (chapter 5).

6.2 KEY FINDINGS

6.2.1 The response of faunal diversity to ecological restoration

This thesis shows that ecological restoration of tropical forests leads to the development of more functionally diverse, rainforest-like faunal communities with a higher total biomass within a relatively short time frame (10-17 years). A shift in faunal species composition was found at around the time canopy closure occurs (2-5 years), highlighting the relationship between faunal community composition and vegetation structure in tropical rainforests (Davis et al. 2002, Williams et al. 2002).

The recovery of faunal communities in older restoration sites may represent an increase in colonization opportunities as restoration sites get older. The increase in biomass of mammals and dung beetles in restored sites, is supported by previous studies (Barnes et al. 2014, Hernandez et al. 2014) and suggests that the carrying capacity of restored sites is higher than that of degraded pasture, but is still limited compared to rainforest.

A decrease in dung beetle functional evenness along with an increase in functional and species richness with restoration age indicates that although there are potentially high levels of competition in older restoration sites, these sites contain more resources to enable competitive groups to co-exist (Mouchet et al. 2010, Pakeman 2011). Indeed, the increase in total biomass of mammals in older restored sites represents an increase in dung deposition and so more available food resources for dung beetles (Hanski and Cambefort 1991, Andresen and Laurance 2007). Conversely, there was an increase in mammal functional dispersion with restoration age, indicating a higher degree of niche differentiation, and thus low resource competition in the older restoration sites, suggesting that niche complementarity is enhancing mammal species’ occurrence probabilities or abundances (Mason et al. 2013).

6.2.2 The response of ecosystem functions to ecological restoration

Cross-chapter findings reveal that ecosystem functions of tropical forests can recover in a relatively short time frame (10-17 years), following ecological restoration (chapter 3, 4 and 5). Litter in litterbags including macrofauna decomposed faster than in litterbags excluding macrofauna, demonstrating the importance of larger invertebrates in litter decomposition processes (chapter 4). Soil macrofauna are known to disaggregate litter and increase the surface area of leaves and twigs for smaller invertebrates to use, thereby promoting decomposition (Coleman et al. 2004, Bardgett 2005). As such, the recovery of litter decomposition rates in restored sites is likely to be strongly influenced by the recovery of soil biota. Effective litter decomposition is crucial in forest recovery as it mineralises nutrients, making them available to plants, and also improves soil quality (MacLean and Wein 1978, Moore et al. 2006). An increase in the input of nutrients from decomposing leaf litter aids forest successional recovery in restored forests since litter decomposition is the main pathway for nutrient cycling in terrestrial systems (Vitousek 1984, Aber and Melillo 1991, Coleman and Crossley 1996, Sayer 2006).

The higher levels of dung beetle functional dispersion and evenness in mid-age restoration sites reported in this study (chapter 3) suggest that there is more niche complementarity and less competition between functional groups, which is leading to increased functioning. Increased dung beetle mediated secondary seed dispersal in older restoration sites may benefit seed survival and establishment (Nichols et al. 2007), having a positive impact on plant recruitment and successional recovery of restoration plantings.

6.2.3 The use of diversity metrics

This thesis reveals that functional trait-based metrics show patterns of recovery with restoration age when traditional species-based metrics fail to show clear responses (chapter 2). Furthermore, functional trait-based indices are better predictors of functionality than species richness or abundance (chapter 3), corresponding with previous studies (Mouillot et al. 2011, da Silva and Hernández 2015). Since species richness measures do not reflect functional or ecological differences that determine species-specific response patterns, as well as the functional implications of species loss, they can therefore lead to misleading conclusions about trends in biodiversity (Dunn 2004, Mouillot et al. 2013, Derhé et al. 2016). Functional trait-based metrics are better predictors of ecological functions than traditional species-based metrics, since they capture differences in species' morphology, life-history traits and ecological niches (Gerisch et al. 2012). The findings from this thesis reveal that traditional species-based metrics of diversity are insufficient to assess the success of ecological restoration and functional diversity measures should therefore be used as a complementary tool to investigate species distribution and recovery, since they better explain the mechanistic link between organisms, ecosystem resource dynamics and the ecological processes that they govern (chapter 3). This study also shows that the relationship between restoration age, diversity and ecosystem functioning is not straightforward and depends on the functions, traits and metrics used.

6.2.4 Key drivers of biodiversity and functionality recovery

Biodiversity and functional recovery is influenced by the interaction of factors at multiple spatial scales from the microsite to the landscape (chapter 5). The recovery of faunal diversity in restored forests was driven by increased structural complexity of the vegetation, the establishment of microhabitats with a variety of food and shelter resources and the creation of more stable, less hostile microclimatic conditions. The recovery of functionality, however, was a more complex process, driven by a combination of habitat structure and microclimate, along with landscape context and intrinsic site conditions. The complexity in this response is most likely due to the recovery of stable ecosystem functions requiring multiple species, and often multiple, interacting functional groups, each of which have their own ecological requirements and responses to biophysical parameters (Naeem and Wright 2003, Naeem et al. 2009). For example, dung beetles removed dung at a lower rate in smaller fragments and those surrounded by less rainforest than in larger fragments with more surrounding rainforest (chapter 5). These results are supported by other tropical studies showing effects of fragmentation on dung beetle assemblage structure (Davis et al. 2001, Estrada and Coates-Estrada 2002, Scheffler 2005). The findings from this thesis suggest that although landscape context and intrinsic site characteristics affect restoration success, they can be mitigated to a degree by the establishment of a well-developed, rainforest-like habitat structure and microclimatic conditions within restored sites.

6.3 FUTURE WORK AND RECOMMENDATIONS

This thesis has contributed to the understanding of the mechanistic drivers and patterns of response of biodiversity and functionality to ecological restoration, but it has also highlighted areas for further work on the topic. Firstly, the applicability of these findings for other taxonomic groups and ecosystem functions should be investigated, to determine whether these patterns of response are unique to the study taxa, functions and area or whether they have wider applications. This can be done by replicating the study design in other regions and with other components of biodiversity and their associated functions. Secondly, this thesis has shown the effect of relatively young ecological restoration plantings, but the response of more long-term studies would be useful in assessing whether the recovery trajectories reported here have longer-term effects on the stability and functioning of restored ecosystems. Since this thesis has highlighted the importance of vegetation structure and microclimate on the recovery of restored plantings, studies looking at the effect of pre- and post-restoration management (including site preparation, weed control, frost protection, etc) on vegetation recovery, as well as on biodiversity and functional recovery, is recommended. This would enable land managers to make more informed decisions on best practice in terms of restoration management, and on achieving the goals of restoration, whether for ecosystem service provision, mitigating biodiversity losses, or improving functionality. This study also advocates for continued monitoring of restoration projects, which are generally monitored for the first few years only, due to funding constraints. Ongoing monitoring of restoration plantings enables land managers to assess the restoration trajectory of their planting and identify whether any management interventions are needed. The incorporation of landscape context and site characteristics into the planning of restoration projects is also highlighted in this thesis (chapter 5). It is important that restoration practitioners and land managers account for landscape context and pre-restoration site conditions when making decisions on when and how to restore tropical forests, since restoration success is influenced by factors at multiple spatial scales, and higher order factors impose constraints at lower levels.

As shown in chapter 3, the presence or abundance of a group of organisms (in this case dung beetles) does not necessarily indicate that the ecological functions that they are normally associated with have attained the desired level in restored areas (e.g. dung removal, soil excavation). As such, restoration practitioners should exercise caution when using biodiversity patterns as surrogates of ecosystem function. Empirically testing the response of biodiversity and functionality is recommended, rather than using one as a proxy for the other. This further emphasises the need to use a variety of ecologically meaningful diversity metrics when investigating the mechanisms between biodiversity and functional recovery. Likewise, a key finding of this thesis is the value of functional trait-based indices when exploring diversity responses. Functional trait-based metrics provide a trait-based, causal view of community diversity that captures differences in species' morphology, life-history traits and ecological niches, and are thus better predictors of ecological functions than species-based metrics (chapter 3). Functional diversity indices complement traditional taxonomic based indices (Cadotte et al. 2011, Montoya et al. 2012), so this thesis recommends the use of both diversity indices, along with assessments of ecological functions, to provide comprehensive evaluations of the success of restoration projects. Finally, cross-chapter findings highlight the importance of using reference (target) and degraded sites in studies of restoration success. It is necessary to compare patterns of recovery with values from reference sites in order to assess whether restoration sites are converging on, or deviating from, the target state (SER ISPWG 2004, Ruiz-Jaen and Aide 2005).

6.4 CONCLUDING REMARKS

Species vary in their life history, ability to tolerate disturbance, dispersal abilities, and contribution to ecosystem functions (Swihart et al. 2003, Bonier et al. 2007, Laliberte et al. 2010). Similarly, ecosystem functions operate at different scales, are mediated by different organisms and are influenced by different biotic and abiotic factors (Hooper et al. 2005, Duffy 2009, Cardinale et al. 2012, Vitousek et al. 2013). As such, the responses of different taxa and functions to restoration efforts are likely to vary widely. Furthermore, not all species contribute equally to all functions and the mechanisms driving high functioning levels vary among the traits, functions and taxa considered (Naeem and Wright 2003, Gagic et al. 2015), as well as the environmental context (Steudel et al. 2012, Griffiths et al. 2014). Despite this, the majority of studies looking at the success of restoration focus on a single taxon or function in isolation, and are therefore unlikely to be capturing these complexities. The findings of such studies, therefore, may not be representative of other components of biodiversity or ecosystem functions, and are likely to be inappropriate for drawing general conclusions about the success of restoration. Consequently, this thesis has taken a multi-trophic level approach in an attempt to make the findings of this study more applicable to other taxa (both invertebrate and vertebrate); and has used a variety of ecologically meaningful diversity metrics to provide a more mechanistic link between the responses of biodiversity and functionality. An assessment of several ecosystem functions relating to nutrient cycling and successional recovery were simultaneously investigated alongside biodiversity, to better understand the causal factors behind recovery and provide a robust framework for the assessment of ecosystem recovery in response to ecological restoration.

Overall, this thesis provides strong support for the use of ecological restoration as a viable way to recover rainforest biota and processes in a relatively short time frame.

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